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LIMNOLOGY AND TROPHIC ECOLOGY OF SOME ALASKAN SUBARCTIC LAKES

University of Alaska M.S. 1984

LIMNOLOGY AND TROPHIC ECOLOGY OF SOME ALASKAN SUBARCTIC LAKES

A

THESIS

Presented to the Faculty of the University of Alaska

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

by

Leonard J. Vining III, B.S.

Fairbanks, Alaska

May 1984

LIMNOLOGY AND THE COMMUNITIES OF

BENTHIC MACROINVERTEBRATES OF SOME ALASKAN

SUBARCTIC LAKES

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ABSTRACT

This study was undertaken to provide a basis for evaluating effects of the proposed Northwest Alaska Natural Gas Pipeline through a permafrost region in interior Alaska. Physical and chemical characteristics of 9 lakes hydrologically connected to a creek were compared to those of 6 lakes hydrologically isolated from the creek. Isolated lakes were warmer and had lower pH, alkalinity, hardness and reactive phosphorus than connected lakes. In two of the 15 lakes (Lakes 10 and 17), community structure of benthic macroinvertebrates was numerically and volumetrically compared by taxa and functional feeding groups. Lake 10 possessed abundant macrophytes but few fish, whereas, Lake 17 contained a dense population of humpback whitefish (Coregonus pidschian) which primarily consumed Chironomidae and Cladocera. The relatively greater numbers and biovolumes of large taxa (e.g. Odonata, Conchostraca), shredders (e.g. Limnephilus) and predators (Odonata, Dytiscidae, Gyrinidae) in Lake 10 was attributed to the greater abundance of macrophytes and lack of fish predation.

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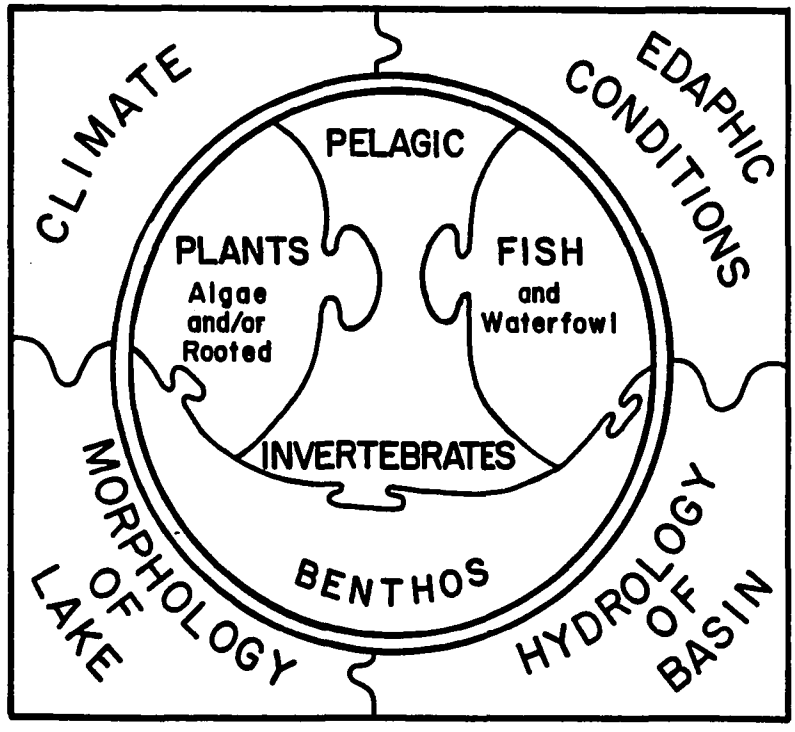
GENERAL INTRODUCTION

This research project began, in 1979, as part of a waterbird study along the proposed gas pipeline corridor near the intersection of the Alaska highway and the Canadian border. The area supports a relatively dense population of waterbirds (Spindler and Kessel 1977) and it was feared that construction activities might adversely impact waterbird production or aquatic habitat in general. Therefore, the waterbird study was undertaken to provide a basis for evaluating potential effects of construction of the Northwest Alaskan Natural Gas Pipeline through the region.

I was responsible for the limnological section of that study. The objectives for that study were expanded in 1980 to include three major components: physical/chemical limnology, lake invertebrates and fish.

A general conceptual model of a lake ecosystem is presented in Figure 1. Four primary factors; 1) climate, 2) edaphic conditions, 3) basin hydrology and 4) lake morphometry were viewed as the primary determinants governing physical and chemical limits within which the lake biota exist. For the purposes of this study, biotic components of the lake were divided into four basic compartments: 1) algae and/or rooted plants, 2) pelagic invertebrates, 3) benthic invertebrates (benthos) and 4) fish. Each component was viewed as an interrelated part of the lake ecosystem.

A traditional "lake typology" approach was used (Brinkhurst 1974). Fifteen lakes in the region were characterized according to their physical and chemical properties. The invertebrate section was more specific, contrasting the benthic macroinvertebrate communities of two



LAKE ECOSYSTEM

Figure 1. Internal and external components of a generalized lake ecosystem.

lakes (Lakes 10 and 17) in terms of their taxonomic and functional (feeding mode) organization (Merritt and Cummins 1978).

The nature of carbon sources (Vannote et al. 1980) and predaceous fish (Zaret 1980) are known to play pivotal roles in structuring aquatic invertebrate communities. Lake 10 possessed considerable amounts of rooted aquatic macrophytes but negligible fish populations. In contrast, Lake 17 contained virtually no macrophytes but possessed a dense population of humpback whitefish (Coregonus pidschian). Differences in invertebrate community structure and taxonomic organization of the two lakes were interpreted in light of these fundamental differences.

The primary objectives were to:

1) provide general limnological information on some taiga lakes in interior Alaska,
2) document and compare the taxonomic and functional (feeding mode) organization of the benthic macroinvertebrate communities in two contrasting lake types, and
3) provide new information on the feeding behavior of humpback whitefish.

Following the introduction and the general study area description, there are three sections entitled Limnology, Fish Study, and Invertebrate Study. Overlap of material in each section has been kept to a minimum. The final Summary/Conclusions section is a condensation of material from all sections.

STUDY AREA

GENERAL

The study area is located in the upper Tanana River Valley (NE portion of the Nabesna quadrangle in east central Alaska, at an approximate latitude and longitude of N 62° 38' and W 141° 10', (Figure 2). Two brown-water[1] creeks (Scottie Creek and Desper Creek) meander through the area and drain into the Chisana River, which constitutes a main headwater fork of the Tanana River, a main tributary of the Yukon River.

In Alaska, the two principal lake-forming processes involve glacier ice and permafrost (Livingstone 1963, Hutchinson 1975). However, since nearly all the region of interior Alaska between the Brooks Range and the Alaska Range was unglaciated during the Quaternary (Ager 1975), permafrost conditions are the dominant factor accounting for the profusion of shallow thaw lakes throughout interior river valleys (Livingstone 1963). The study area is located along the edge of an outwash fan protruding northward from the foothills of the Alaska Range (Ager 1975). The general area is underlain with permafrost (Selkregg 1976) and fine-grained sediments (Wallace 1948) and is a mosaic of meandering creeks and numerous, shallow lakes amid an alternating terrestrial habitat of coniferous forest and bog.

Desper and Scottie Creeks constitute major structural features of the landscape, hydrologically connecting a series of small lakes (for detailed map, see Kessel et al. 1980). Of approximately 100 small

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[1] Brown-water is probably due to the presence of humic compounds.

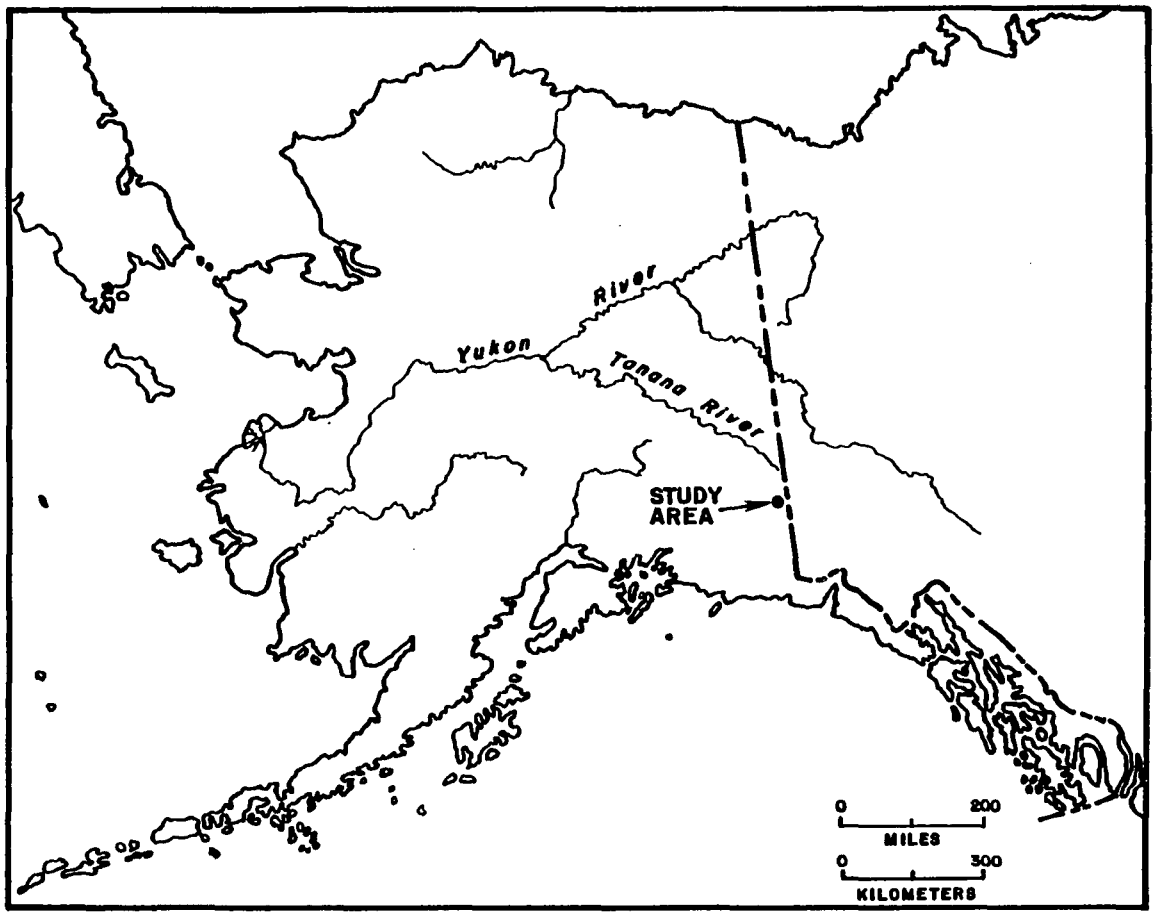

Figure 2. Map of Alaska. Arrow indicates location of Scottie-Desper Creeks Study Area.

lakes scattered throughout the study area, about half are hydrologically connected to a creek via surface channels and appear to have been formed by the sinking of unfrozen pockets of the permafrost basin (Wallace 1948). According to Wallace, under present climatic conditions, small depressions formed in this manner fill with water and continue to increase in size via thermal conductance and continued melting of permafrost. The embryo lakes enlarge and fuse into a complicated series of large connected basins and eventually become isolated again via a system of levees that form along the water courses.

The composition and distribution of isolated and connected lakes in the Scottie-Desper Creeks Study Area appear to fit the scheme proposed by Wallace. Most lakes are expanding and coalescing with no large lakes isolated via levees.

WEATHER

Principal characteristics of the subarctic environment are extremely long, cold winters and short summers, accompanied by an eccentric light regime and relatively low amounts of precipitation. The light regime of the Scottie-Desper Creeks Study Area undergoes large variations from 4.5 hours of daylight on 22 December to 20.5 hours of daylight on 22 June (plus approximately 3.5 hours of twilight at both dates (Hartman and Johnson 1978)).

The period of permanent snow cover varies from year to year but generally extends from early October to the end of April. The ice-covered period for most lakes in the area is roughly seven months. In

1979, most lakes were ice-free by the first week in May (except Lake 17), and were icing-over by early to mid-October. A more detailed account of spring break-up in this area is given in Kessel et al. (1980).

Typically, most precipitation falls as rain during June and July (Figure 3) with a total annual precipitation of approximately 26 cm (Hartman and Johnson 1978). Although the total annual precipitation is relatively low, its influence on creek and lake water levels is magnified by the timing of rainfall and the presence of permafrost underlying the area. Because of its impermeability, permafrost undoubtedly has a great influence on the hydrological cycle in this area. An atypical precipitation pattern during the summer of 1979 resulted in flood conditions in July (Figure 3). All months except July were dryer than normal. July precipitation was 2.84 cm above the 10-year mean, resulting in extensive water-level fluctuations in Scottie Creek (the water level rose approximately 4 meters in a two week period) and associated lakes.

FLUVIAL HABITAT

Desper and Scottie Creeks meander through much of the study area before merging and draining into the glacially-fed Chisana River. Both Desper and Scottie Creeks are bog-fed channels (containing brown water) that experience substantially higher water levels following rains. However, they differ in several respects. Scottie Creek is a deep, high volume creek (12.97 $m^3 s^{-1}$ in September, 1979; Chihuly et al. 1979) that flows throughout the winter. It has steep banks and very few

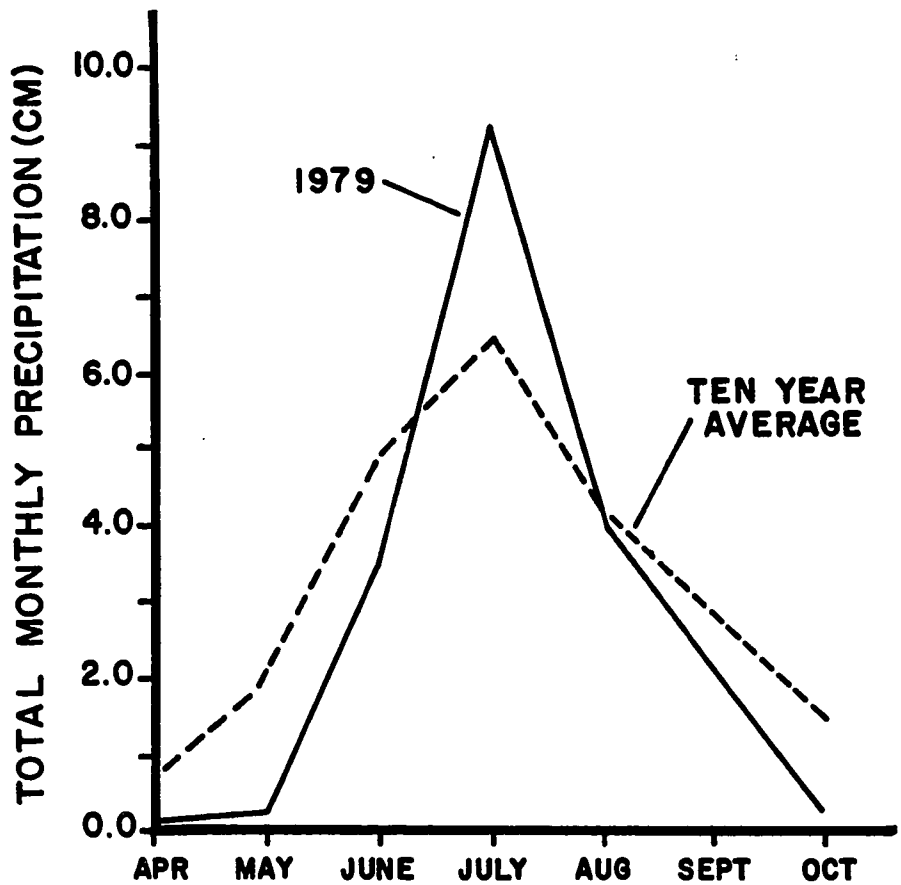

Figure 3. Total monthly precipitation from April to October, 1979, compared with the ten year average (1969-1979). Data collected from Northway Airport, approximately 50 km northwest of the Scottie-Desper Creeks Study Area, Alaska.

submergent macrophytes. Although the banks are forested, they are unstable, probably due to the effects of melting permafrost.

In contrast, Desper Creek is shallow, lower in volume (0.28 $m^3 s^{-1}$ in September, 1979; Chihuly et al. 1979) and probably freezes solid in winter. It supports submergent vegetation in its channel and possesses a variety of emergent plants along its gently-sloping banks.

There are no detailed studies reporting seasonal usage patterns of fish in these creeks. Chihuly et al. (1979) reports that Desper Creek is used by northern pike (Esox lucius) during the ice-free period. Because this creek presumably freezes in winter (depth approximately 1.0 m), use by fish is restricted to the ice-free period. Scottie Creek is reportedly used by burbot (Lota lota), longnose suckers (Catastomus catastomus) and Arctic grayling (Thymallus arcticus) (Chihuly et al. 1979; Tack 1980). In addition, local residents report that whitefish are present in the creek in spring and fall. These fish are likely to be humpback whitefish, because this species was captured in significant numbers during 1980 in the lower portions of the drainage [(Lake 17), this study]. It is likely that these creeks are used by fish primarily as access corridors to spawning and/or feeding grounds.

LACUSTRINE HABITAT

Lakes varied considerably in surface area and shape, but were generally uniformly shallow in depth (1.0-3.0 m). Lake margins supported a variety of plant types. Some shorelines were abruptly defined by dense stands of willow (Salix spp.), but generally, margins

were formed by stands of Carex rosteata or C. aquatilis. These stands ranged from thin bands along the poorly developed shorelines of isolated lakes to extensive meadows around larger connected lakes. Common forbs such as buckbean (Menyanthes trifoliata), marsh marigold (Caltha palustris), wild calla (Calla palustris), and marsh fleabane (Senecio congestus) were often found in thin bands along poorly developed shorelines (Kessel et al. 1980).

Isolated and connected lakes were observably different in size, water clarity and biotic community composition. Isolated lakes were generally smaller, had poorly developed littoral zones, few submergent vascular plants, clear water and few observable macroinvertebrates. The dominant aquatic plants were pond lillies, Nuphar polysepalum and to a lesser extent, Nymphea tetragona (Kessel et al. 1980). Connected lakes were more variable but generally had well-developed littoral zones, dense beds of submergent vascular plants, humic stained water and a greater abundance of observable macroinvertebrates. The most abundant vascular plants were water milfoil (Myriophyllum spicatum), several species of pondweeds (Potamogeton vaginatus, P. gramineus, P. pectinatus, P. perfoliatus and Zanichellia palustris), bladderwort (Utricularis spp.) and water smartweed (Polygonum amphibium) (Kessel et al. 1980). In addition, blooms of Aphanizomenon sp. were present in connected lakes but noticeably absent in isolated lakes.

LAKES 10 AND 17

Lakes 10 and 17 (Figures 4 and 5) were selected for more intensive investigations of their limnological characteristics and benthic invertebrate communities. These lakes were located approximately 1 km

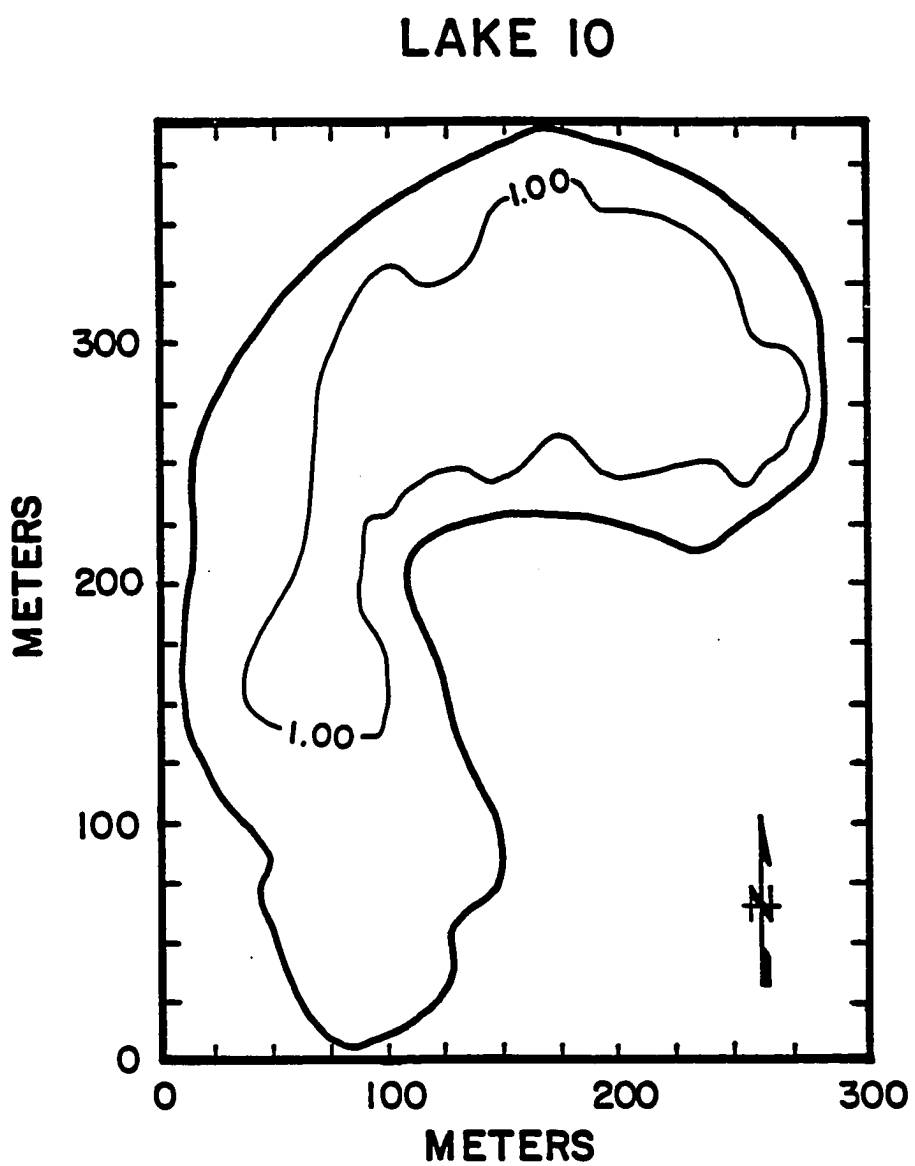

Figure 4. Bathymetric map (1.0 m contour intervals) of Lake 10, Scottie-Desper Creeks Study Area, Alaska, 1979 (N 62° 39' 21"; W 141° 9' 20").

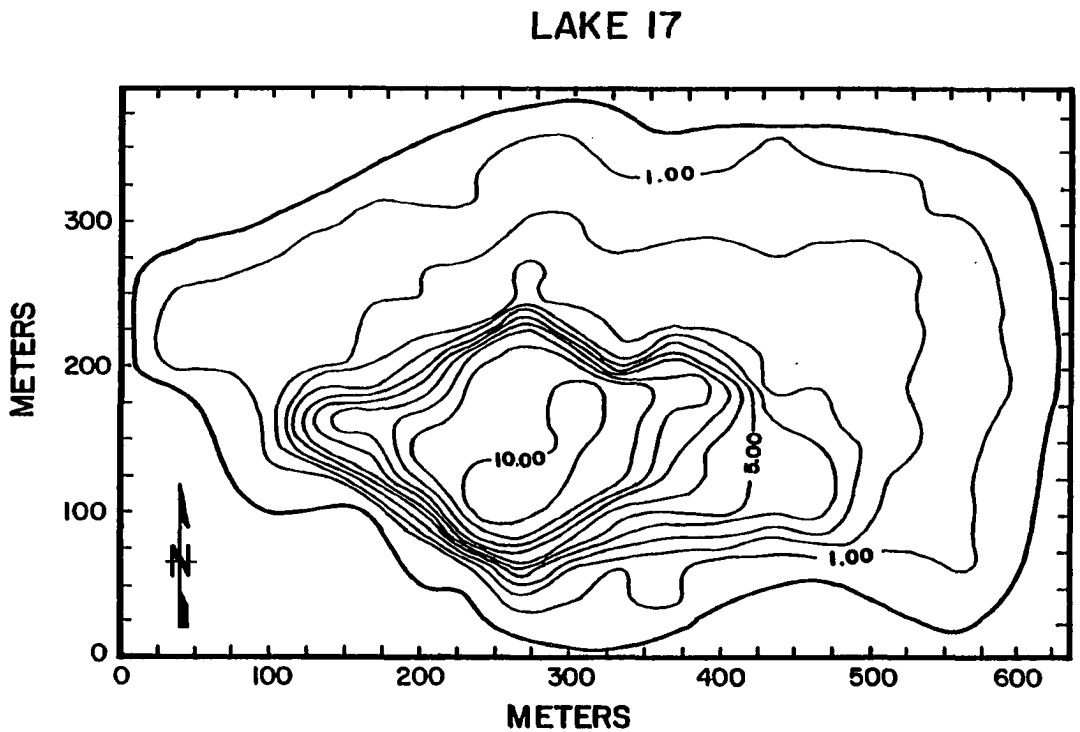

Figure 5. Bathymetric map (1.0 m contour intervals) of Lake 17, Scottie-Desper Creeks Study Area, Alaska, 1979 (N 62° 38' 55"; W 141° 10' 37").

apart and both were connected to Scottie Creek. However, they differed in several ways. Lake 10 was a small (8.3 ha), shallow (maximum depth = 1.6 m) bean-shaped lake containing large amounts of emergent (Carex spp.) and submergent (Potamogeton spp.) macrophytes but essentially no fish. In contrast, Lake 17 was much larger (26.9 ha) and deeper (maximum depth = 10.5 m) was elipsoid in shape and contained a relatively dense population of humpback whitefish, but few macrophytes. Although there were few macrophytes present, there was a persistent bloom of the blue-green algae, Aphanizomenon sp., from mid-June to mid-August. This bloom underwent a dramatic collapse in September 1979, resulting in a large pulse of dead organic material to the sediments.

A beaver dam at the outlet of Lake 10 restricted hydrological influences of Scottie Creek to times of periodic high water levels. This dam apparently blocked fish access, because no fish were observed in 1979 and only fingerlings of longnose suckers (Catastomus catastomus) were captured in 1980. Presumably, a few adult suckers gained access during high-water levels in spring, 1980, then reproduced. However, due to the shallowness (maximum depth = 1.6 m) of the lake, it is almost certain that fish could not successfully overwinter.

Hydrology in Lake 17 was more directly influenced by Scottie Creek via surface channel connections through Lakes 15 and 16. Water-level fluctuations in the creek resulted in corresponding fluctuations in Lake 17. The connections undoubtedly allowed free movements of fish to and from the lake.

LIMNOLOGY

INTRODUCTION

There have been a considerable number of limnological studies on arctic and subarctic lakes [for review see Livingstone (1963), Kalff (1970) and Hobbie (1973 and 1980)]. However, relative to arctic lakes there is less information available that pertains to subarctic lakes, particularly interior taiga lakes. Of the interior lake studies, only lakes of similar geologic history are useful for direct comparison to this study because the geologic history profoundly effects physical, chemical and biological characteristics of lakes (Wetzel 1975).

Many recent investigations have focused upon the productivity of various trophic levels, particularly primary productivity of phytoplankton (Kalff and Knoechel 1978). Reported estimates of total annual phytoplankton productivity for interior taiga lakes are varied, but are generally intermediate between those of arctic and lower latitudes (Alexander and Barsdate 1974). Values for interior lakes range from a low 11 $gC \cdot m^{-2} \cdot year^{-1}$ for Smith Lake (Alexander and Barsdate 1971) to a high of 70 $gC \cdot m^{-2} \cdot year^{-1}$ for Ace Lake (Alexander and Barsdate 1974). In contrast, values for arctic lakes vary from 0.3 to 12.5 $gC \cdot m^{-2} \cdot year^{-1}$ (Hobbie 1980). Productive lakes at lower latitudes may exceed 300 $gC \cdot m^{-2} \cdot year^{-1}$ (Wetzel 1975).

There are only a few studies of small shallow lakes in interior Alaska (Likens and Johnson 1968; Alexander and Barsdate 1971, 1974; Barsdate and Alexander 1971), yet vast expanses of lowland river

valleys throughout Alaska are dominated by this lake type. These lakes afford some of the richest waterfowl habitat in the state (Kessel et al. 1980) and are undoubtedly used by a variety of fishes for spawning and/or feeding.

OBJECTIVES

This study was undertaken to extend baseline information on the limnology of taiga lakes in interior Alaska. Variations in the limnological composition of lakes within the region were analyzed with regard to morphological features known to be important in controlling the limnology of lakes. The study objectives were to:

1) characterize lake types on the basis of physical and chemical variables,
2) interpret patterns in the limnological data in terms of geologic and morphometric constraints and
3) provide a detailed description of the limnology of two lakes that would aid in understanding differences in the structure of their benthic macroinvertebrate communities.

METHODS

Fifteen lakes were selected as representative of lakes in the study area. Selections were made subjectively to ensure reasonable accessibility and to provide a range in size and hydrologic association (isolated or connected) to Scottie Creek. Data were collected from all 15 lakes in 1979, but only from two lakes in 1980.

PHYSICAL VARIABLES

TEMPERATURE

Replicate surface temperatures were obtained with a standard hand thermometer; readings were taken immediately upon withdrawal of a small sample.

WATER TRANSPARENCY

Measurements were made by submerging a 20 cm secchi disc from the shaded side of the canoe. Because of variable environmental conditions (time of day, roughness of water, cloud cover, shallowness of lakes, etc.), transparency readings were grouped into three classes: Class 1 < 1.0 m; class 2 = 1.0 m to 2.0 m; and class 3 > 2.0 m. Class 3 included some shallow, clear lakes that were less than 2 m deep.

SURFACE AREA

Lake surface areas were obtained from data reported in Kessel *et al.* (1980).

DEPTH

A lead sounding line was used to obtain depths of Lakes 10 and 17. Ten transects were taken on each lake. Since both lakes had soft mud bottoms, care was taken to minimize over-estimating depth due to the sinking of the weight into the sediments. Depth contours were generated with the aid of a computer contouring program (Sampson 1978; Surf II). Lake perimeters were mapped by the plane-table method described in Lind (1974).

CHEMICAL VARIABLES

All water samples for determination of chemical variables were collected from the surface. Samples were obtained either from a canoe with a brass Kemmerer water sampler (1 liter capacity) or by wading to a depth of 0.5 to 1.0 m and submerging a polyethylene container by hand. Care was taken to avoid material trapped in the surface film.

CONDUCTIVITY

Conductivity readings were taken with a field meter from Hach Chemical Company (model 17250). However, not all data were used due to malfunctioning of the meter.

TOTAL ALKALINITY, TOTAL HARDNESS AND DISSOLVED OXYGEN

A digital titrator (Hach Chemical Company) with prepackaged titrants was used to determine total alkalinity (t-alkalinity), total hardness (t-hardness) and dissolved oxygen. Titrations were performed in accordance with specifications provided by the Hach Chemical Company.

Total alkalinity was determined using 1.589 N and 0.1589 N sulfuric acid titration cartridges. Phenolphthalein and bromcresol green-methyl red were used as the colorimetric endpoint indicators at a pH of 8.3 and 4.5, respectively.

A 0.794 N EDTA titration cartridge was used for all hardness titrations. Water samples were prepared for titration by adding 1 ml of buffer solution, followed by a prepackaged amount of ManVer II (Hach Chemical Company) hardness indicator.

In 1979, the Azide Modified Winkler method was employed for determinations of dissolved oxygen (DO). However, due to incorrect concentrations of reagents, data for saturated DO levels were faulty and discarded. In 1980, DO determinations were made with an oxygen meter (Yellow Springs Instrument Company, model #57). It was calibrated in the field using the Azide Modified Winkler method.

NITRATE, NITRITE, AMMONIA, PHOSPHATE AND SILICON (dissolved forms)

All collecting equipment was double-washed with 10% HCl, followed by six rinses with double-deionized water. Each sample was obtained as follows: 1) a 150-200 ml water sample was filtered through a Gelman glass fiber filter (0.47 µm nominal retention) into a 120 ml polyethylene bottle, leaving it only three-fourths full to allow for expansion during freezing; 2) three to five drops of 10% mercuric chloride were added as a preservative and the samples were stored in the shade until they could be frozen (within 2 to 5 days); and 3) samples in the polyethylene bottles remained frozen until the time of analysis, a maximum period of about 6 months. Laboratory analyses of

the dissolved fractions of each limnological variable were performed with a continuous flow autoanalyzer (Technicon AutoAnalyzer II), following procedures outlined in Whitledge et al. (1981).

ACIDITY

Spring pH readings were obtained with a Sargent Welch meter (model RB). A Van Waters and Rogers meter (model #55) was used during fall sampling. While in use, both meters were frequently standardized with buffers of known pH.

STATISTICAL PROCEDURES

Data from spring and fall were combined into a single data set. Because units of several variables were different, the data were standardized to Z scores (Davis 1973). Although 15 limnological variables were measured, not all were included in subsequent analyses. Conductivity data was not included because of suspected meter malfunctioning and its lack of significant correlation with either t-hardness or t-alkalinity. Dissolved oxygen measurements were discarded from multivariate analyses due to a problem with chemical titrants. However, some dissolved oxygen data was valid and reported as depth profiles.

A cluster analysis (Dixon and Brown 1979: BMDP-2M) was performed using "lakes" as the grouping variable and Euclidean distance as the measure of similarity. In addition, a principal component analysis (Ortho B rotation of Dixon and Brown 1979: BMDP-4M) was performed.

RESULTS

GENERAL PATTERNS

Mean values of limnological variables for each lake are presented in Appendix Table A-1. Principal components analysis (PCA) was used to analyze patterns of variation in the data set. In the analysis, 11 limnological variable were reduced to three principal components that accounted for 80% of the total variation (Figure 6). Component I accounted for 33% of the variation and was most heavily influenced by phosphate, pH, alkalinity, hardness and temperature. Depth, area and silicon loaded most heavily on Component II, which accounted for an additional 24% of the variation. Nitrogen fractions (nitrate, nitrite and ammonia) contributed most heavily to Component III, which accounted for 23% of the total variation (see Appendix Table A-2 for factor loadings). The limnological data for each lake was projected onto the three principal components by plotting the centroids of factor scores along the principal component axes (Figure 6). Lakes were separated into two basic groups primarily on the basis of Component I. The two groups corresponded to two types of lakes, distinguished by the presence or absence of surface connections with Scottie Creek.

Lakes hydrologically isolated (isolated lakes) were generally warmer and had lower pH, alkalinity, hardness and phosphates than lakes connected to the creek system (connected lakes). Also, isolated lakes were much more tightly grouped than connected lakes, indicating less within-group variation (Figure 6). As a group, connected lakes overlapped with isolated lakes on Components II and III and contained a few

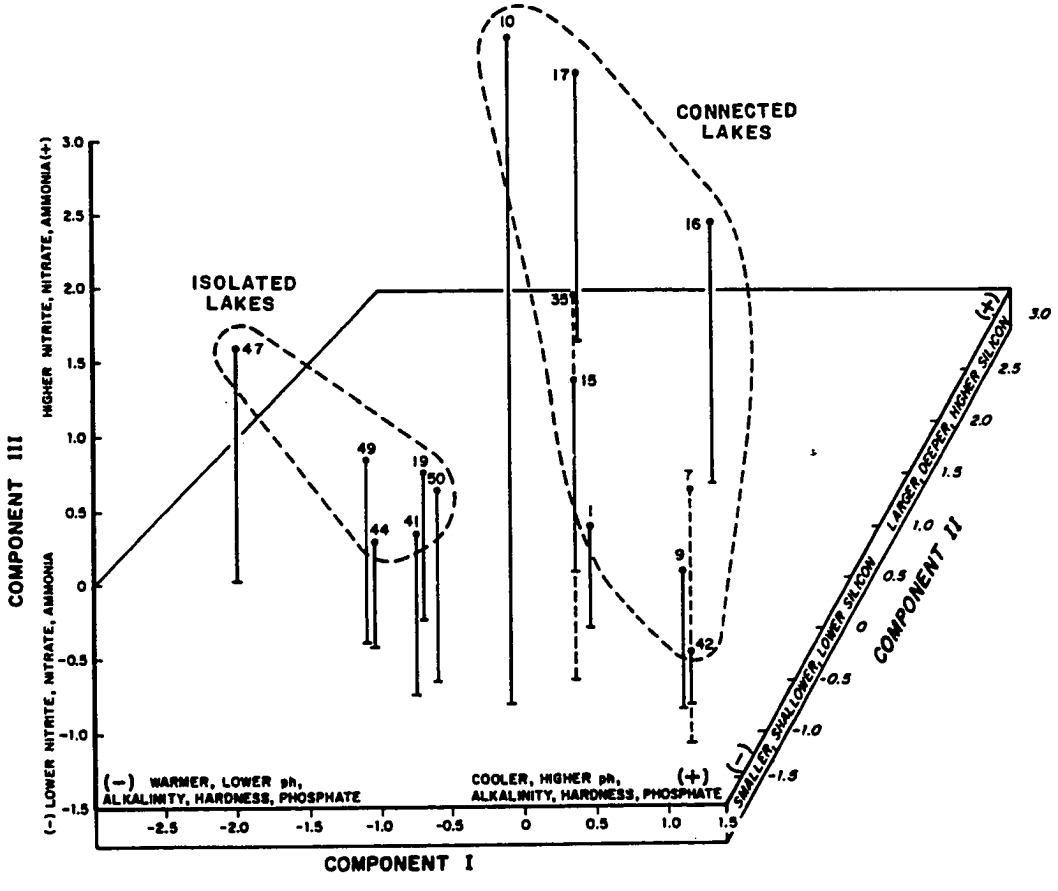

Figure 6. Ordination (based on physical and chemical variables) of six lakes hydrologically isolated from and nine lakes hydrologically connected to Scottie or Desper Creek, Alaska, 1979. Eighty percent of total variation was accounted for by three components; Component I = 33%, Component II = 24%, Component III = 23%.

lakes that were larger, deeper and had higher silicon levels (Component II) as well as higher levels of nitrogen compounds (Component III).

The same data set was analyzed via cluster analysis. The resultant clustering pattern was similar to the ordination pattern of the PC analysis (Figure 7). Two types of lakes (isolated and connected) were distinct. In addition, there was a relatively close correspondence between the order of amalgamation of lakes in the cluster analysis and the location of individual lakes on the ordination axes (Figure 6). For example, Lake 47 was the farthest removed from the rest of the isolated group in the PCA and was the last lake (of isolated lakes) to be amalgamated in the cluster analysis. Also, isolated lakes were arranged in a tighter grouping in the ordination and were amalgamated earlier in the cluster analysis than connected lakes. At the other extreme, Lakes 10, 16 and 17 were widely separated in Figure 6 and were amalgamated late in the cluster analysis. In general, both analyses indicated fundamental differences in limnological characteristics between isolated and connected lakes.

Means of limnological variables for connected and isolated lakes (Table 1) were tested for significant differences (Mann-Whitney U Test: Zar 1974). There were no significant differences ($P > 0.05$) between temperature, area, maximum depth, nitrate and silicon. However, all remaining chemical variables were significantly higher for connected lakes ($P < 0.05$).

Table 2 provides a comparison of nitrate and dissolved reactive phosphorus levels between lakes of this study and other selected lakes of interior Alaska. In general, nutrient levels for lakes of the Scottie-Desper Creeks Study Area were similar to those reported in the

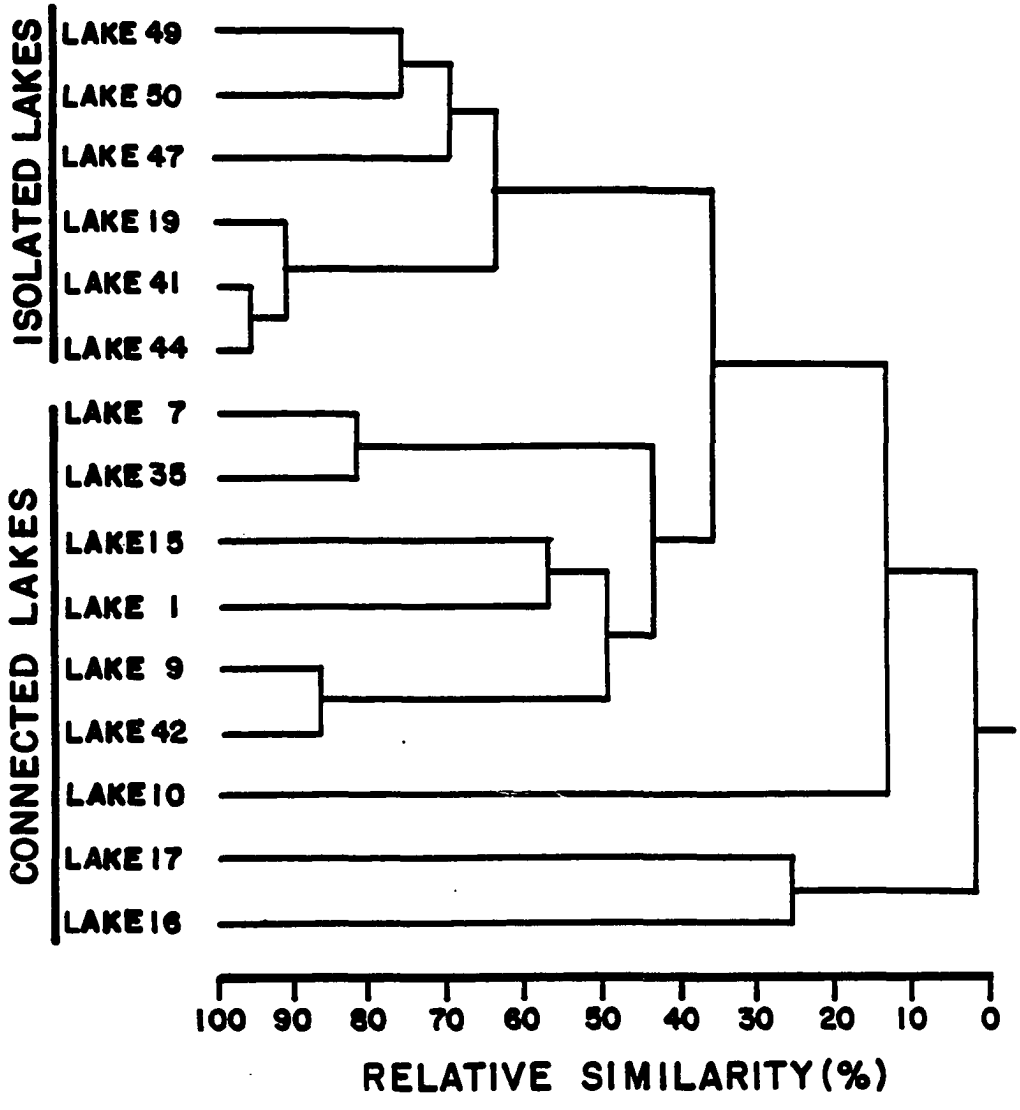

Figure 7. Cluster analysis of physical and chemical characteristics of six lakes hydrologically isolated from and nine lakes hydrologically connected to Scottie or Desper Creek, Alaska, 1979 [alphanumeric codes for lakes are consistent with Kessel et al. (1980)].

Table 1. Means ± SD of limnological variables obtained from 15 lakes during spring (19 June - 4 July) and fall (29 August - 11 September) sampling periods, Scottie-Desper Creeks Study Area, Alaska, 1979. Lake designations (isolated and connected) refer to the hydrological association of lakes to Scottie or Desper Creek.

Variable	All Lakes n = 15	Isolated Lakes n = 6	Connected Lakes n = 9
Temperature (°C)	14.29 ± 1.49	15.41 ± 2.03	13.53 ± 1.01
Maximum Depth (m)	2.85 ± 2.39	2.47 ± 1.25	3.11 ± 2.88
Area (ha)	23.58 ± 26.25	13.72 ± 19.43	30.16 ± 29.73
*pH	7.31 ± 0.27	7.10 ± 0.28	7.50 ± 0.27
*Total Alkalinity ($mgCaCO_3 \cdot liter^{-1}$)	67.67 ± 28.12	35.50 ± 12.90	89.11 ± 34.37
*Total Hardness ($mgCaCO_3 \cdot liter^{-1}$)	66.00 ± 27.73	29.50 ± 15.18	90.33 ± 33.25
Silicon ($ug\text{-}atoms \cdot liter^{-1}$)	27.58 ± 18.15	19.17 ± 7.92	33.18 ± 22.27
*Phosphate ($ug\text{-}atoms \cdot liter^{-1}$)	0.47 ± 0.12	0.20 ± 0.05	0.66 ± 0.15
Nitrate ($ug\text{-}atoms \cdot liter^{-1}$)	1.85 ± 1.40	1.39 ± 0.85	2.16 ± 1.65
*Nitrite ($ug\text{-}atoms \cdot liter^{-1}$)	0.34 ± 0.28	0.16 ± 0.03	0.45 ± 0.36
*Ammonia ($ug\text{-}atoms \cdot liter^{-1}$)	3.78 ± 0.87	2.91 ± 0.36	4.37 ± 1.07

* Isolated and connected lakes significantly different; Mann-Whitney U test; $P < 0.05$.

Table 2. Mean levels of dissolved nutrients in lakes of Scottie-Desper Creeks Study Area, compared to other interior Alaskan lakes. Data derived from literature generally are means of spring, summer and fall. Phosphate refers to dissolved reactive phosphorus. Units are ug-atoms · liter^{-1}.

	Smith*** Lake	Ace* Lake	Deuce* Lake	Tanana** Valley	Lake** Louise	Tangle** Lakes	Scottie-Desper Lakes		
							Connected	Isolated	Combined
Nitrate	0.2	1.4	3.8	0.3	0.3	2.7	2.2	1.4	1.8
Phosphate	0.4	1.4	1.0	0.2	0.02	0.4	0.7	0.2	0.5

* Alexander and Barsdate (1974).
** Barsdate and Alexander (1971).
*** Alexander and Barsdate (1971).

literature. Lakes 10 and 17 were both connected lakes (to Scottie Creek) and were selected for more intensive investigation. Note that they contained relatively high levels of both nitrate and phosphate and had particularly high levels of nitrate compared to other interior lakes.

Although both lakes were connected lakes, they were widely spaced on Component II of the ordination (Figure 6) and were amalgamated late in the cluster dendrogram (Figure 7). Lake 10 had the highest levels of nitrite, nitrate and combined nitrogen. Lake 17 also had relatively high levels of nitrogen compounds (similar to most other connected lakes). In addition, it had the highest silicon level and was more than twice as deep as the next deepest lake.

LAKES 10 AND 17

Table 3 is a summary of limnological data obtained at different times of year from surfaces and maximum depth samples of Lakes 10 and 17. In general, Lake 17 exhibited large and relatively predictable differences in most variables between surface and maximum depth, whereas Lake 10 exhibited less predictable variation. Both lakes were neutral in pH and contained calcium bicarbonate waters. However, the values for t-alkalinity may be overestimated since titrations may be effected by the disassociations of organic salts in highly colored water (Barsdate 1967). In both lakes, values for t-hardness approximated those for t-alkalinity, indicating that anions other than carbonate and bicarbonate were insignificant. Conductivity changed with depth in Lake 17 but differed little with depth in Lake

Table 3. Summary of limnological data for Lakes 10 and 17, Scottie-Desper Creeks Study Area, Alaska, 1979 and 1980.

Lake No.	Date	Depth (m)	Temp. (°C)	pH	Total Alkalinity $mgCaCO_3 \cdot liter^{-1}$	Total Hardness $mgCaCO_3 \cdot liter^{-1}$	Conductivity $\mu mhos\ cm^{-1}$	Silicon $\mu g\text{-atoms} \cdot liter^{-1}$	Phosphorus $\mu g\text{-atoms} \cdot liter^{-1}$	Nitrate $\mu g\text{-atoms} \cdot liter^{-1}$	Nitrite $\mu g\text{-atoms} \cdot liter^{-1}$	Ammonia $\mu g\text{-atoms} \cdot liter^{-1}$	Combined Nitrogen $\mu g\text{-atoms} \cdot liter^{-1}$
17	19 June 1980	0.0	16.0	-	-	-	223	-	-	-	-	-	-
		10.0	4.0	-	-	-	350	-	-	-	-	-	-
17	27 June 1979	0.0	-	7.7	154	160	-	73.40	0.50	2.35	0.46	2.93	5.61
		10.0	-	6.7	309	292	-	111.10	2.40	0.13	0.13	61.80	62.06
17	28 July 1979	0.0	19.8	9.2	116	120	268	41.00	0.31	2.82	0.19	1.16	4.17
		10.0	4.0	7.2	296	245	630	127.40	1.00	0.20	0.21	61.20	61.61
17	22 Aug 1980	0.0	13.0	-	144	-	210	-	-	-	-	-	-
		10.0	4.5	-	292	-	350	-	-	-	-	-	-
17	7 Sept 1979	0.0	10.1	7.4	134	138	268	41.36	0.74	4.52	0.56	5.24	10.32
		10.0	4.0	7.2	256	228	450	64.80	0.56	0.28	0.12	85.00	85.40
10	16 June 1980	0.0	19.0	-	-	-	190	-	-	-	-	-	-
		1.0	17.0	-	-	-	175	-	-	-	-	-	-
10	1 July 1979	0.0	18.0	7.4	104	90	142	14.34	0.68	5.32	1.92	5.40	12.64
		1.0	16.5	7.2	109	104	145	70.97	1.88	7.38	1.40	5.44	14.22
10	28 July 1979	0.0	19.9	7.6	86	74	205	22.23	0.31	1.54	0.40	1.90	3.84
		1.7	15.8	7.4	69	82	188	37.96	0.34	3.58	0.34	11.08	15.00
10	20 Aug 1980	0.0	14.7	-	122	115	-	-	-	-	-	-	-
		1.0	14.0	-	117	114	-	-	-	-	-	-	-
10	7 Sept 1979	0.0	11.3	7.1	77	78	151	39.36	0.53	4.53	0.83	5.96	11.32
		1.0	10.5	7.1	74	76	152	39.45	0.88	4.48	0.90	9.50	14.88

10. Conductivity values in both lakes reflect the same pattern of variation between depths as that shown for t-alkalinity and t-hardness, with higher values at increased depths.

A thermocline was recognizable in Lake 17 at all sampling periods, but was near the bottom (9.0 m) at 28 July and 6 September, 1979 (Figure 8). The effects of a thermocline and low dissolved oxygen levels in the hypolimnion of Lake 17 were manifested in elevated levels of several limnological variables. Figure 9 indicates typical clinograde oxygen curves associated with thermoclines (Wetzel 1975). As temperature and dissolved oxygen levels decreased with depth, conductivity, t-alkalinity and t-hardness levels showed concomitant increases.

Thermoclines and associated low oxygen conditions persisted throughout the summer in the deepest region of Lake 17 (Figure 8). Although the data are incomplete, the effects on chemical variables were apparently profound (Table 3). Ionic variables (t-alkalinity, t-hardness and conductivity) and nutrients (dissolved phosphorus and ammonium) had elevated levels at 10.0 m (the hypoxic region). Nitrate and ammonium levels underwent reciprocal trends reflecting the presence of reducing conditions in deeper water.

Thermal and dissolved oxygen regimes in Lake 10 were not vertically structured in the same manner as in Lake 17. Although seasonal surface temperatures were similar (Table 3) vertical profiles were different. In Figure 10, comparisons between locations, times of day and times of year indicated that dissolved oxygen levels were affected relatively more by local exposure to wind (Figure 10A) than by time of day (Figure 10B) or time of year (Figure 10C).

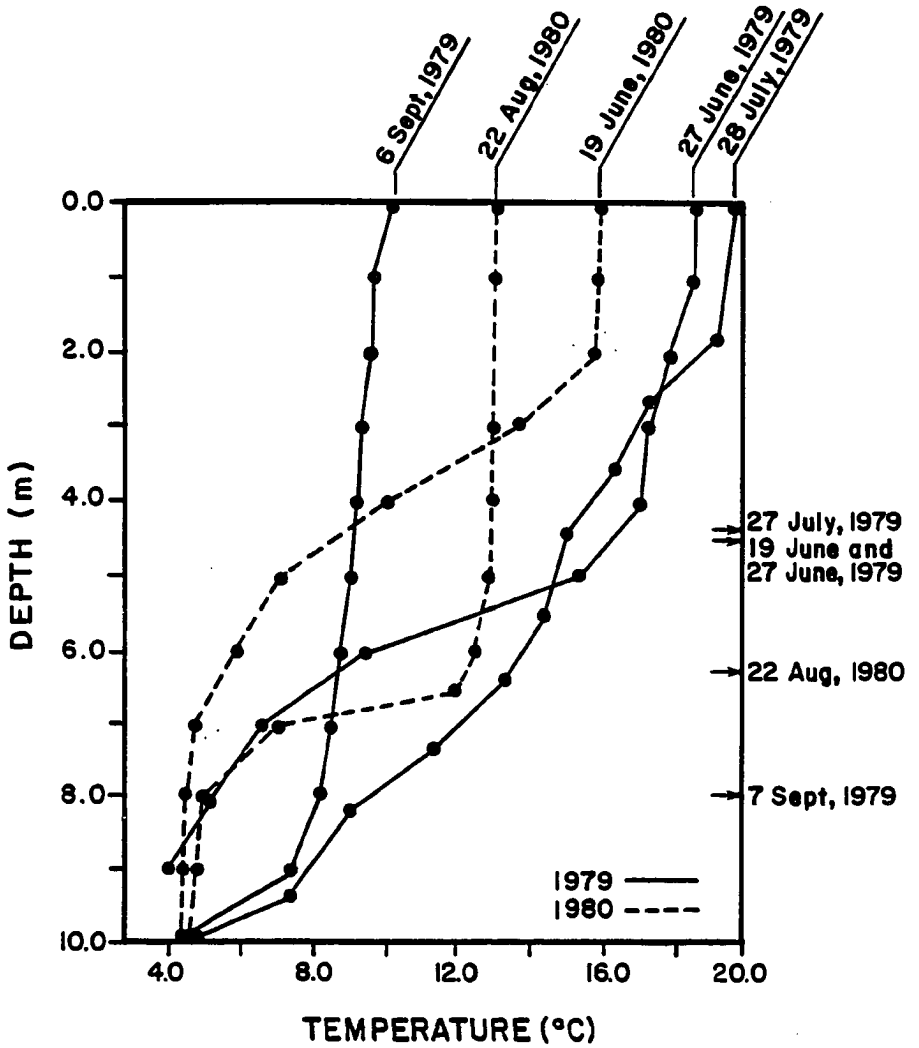

Figure 8. Temperature profiles for Lake 17 at different dates during 1979 and 1980, Scottie-Desper Creeks Study Area, Alaska. Depths at which dissolved oxygen levels are 1.0 mg·liter^{-1} are indicated along right vertical margin.

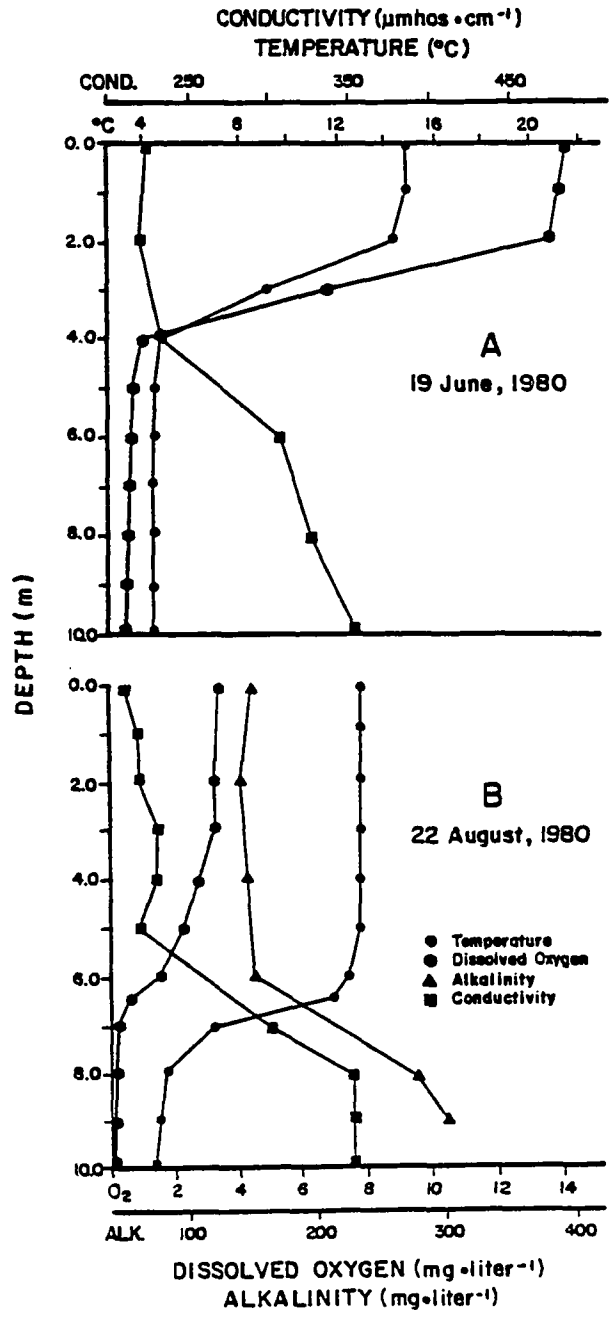

Figure 9. Depth profiles for temperature, conductivity, dissolved oxygen and total alkalinity for Lake 17, Scottie-Desper Creeks Study Area, Alaska, 1980.

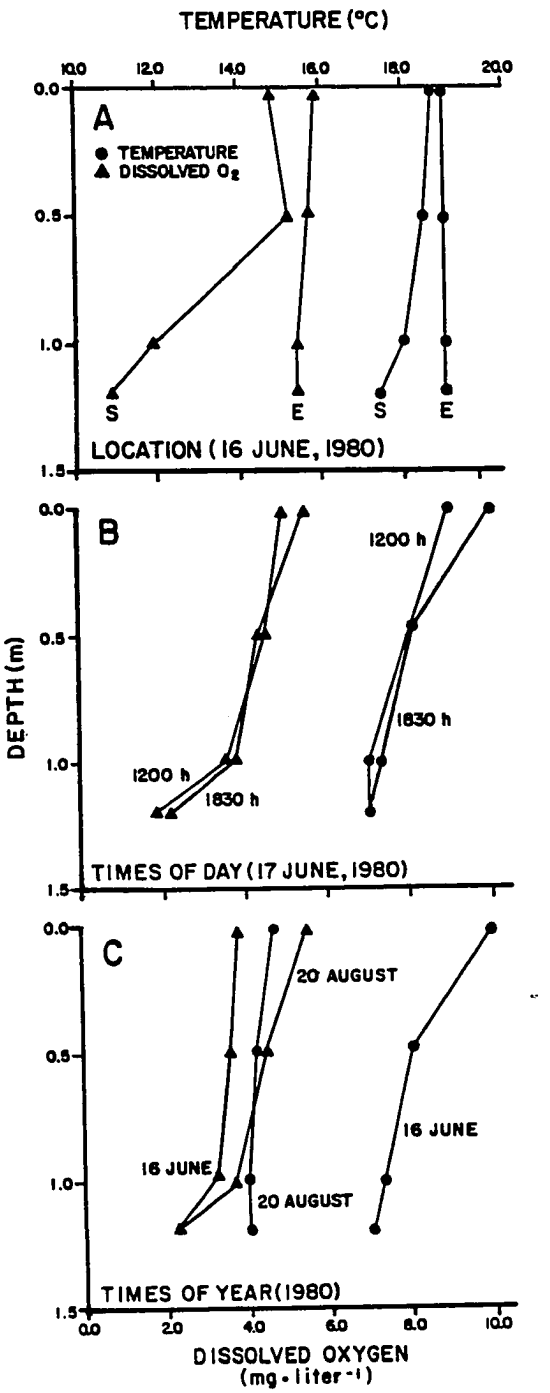

Figure 10. Comparison of temperature and dissolved oxygen profiles at different locations (A), times of day (B), and times of year (C), Lake 10, Scottie-Desper Creek Study Area, 1980. Locations S and E refer to areas sheltered from and exposed to wind, respectively.

Temperature profiles at different times of day (Figure 10B) were generally similar, whereas, sheltered location (S) had consistently lower temperatures at given depths than the exposed location (E) (Figure 10A). Alternatively, there were obvious differences between temperature profiles at different times of year, with late summer values (20 August) being lower than in early summer.

Dissolved oxygen profiles for different locations (Figure 10A) were radically different, with the sheltered area (S) having levels less than 1.0 $mg \cdot l^{-1}$ at a depth of 1.2 m.

The dramatic effect of wind exposure on levels of dissolved oxygen is clearly shown in Figure 11. The increase in concentration of dissolved oxygen was the result of increasing exposure to wind. All readings were obtained at 1.0 m depths as the canoe was slowly blown across the lake from sheltered shore area to the opposite, exposed shore. These data and data in Figure 10A support the notion that local wind conditions and degree of exposure to wind played a substantial role in determining levels of dissolved oxygen in this lake and appear to be more important than diel (Figure 10B) or seasonal (Figure 10C) considerations.

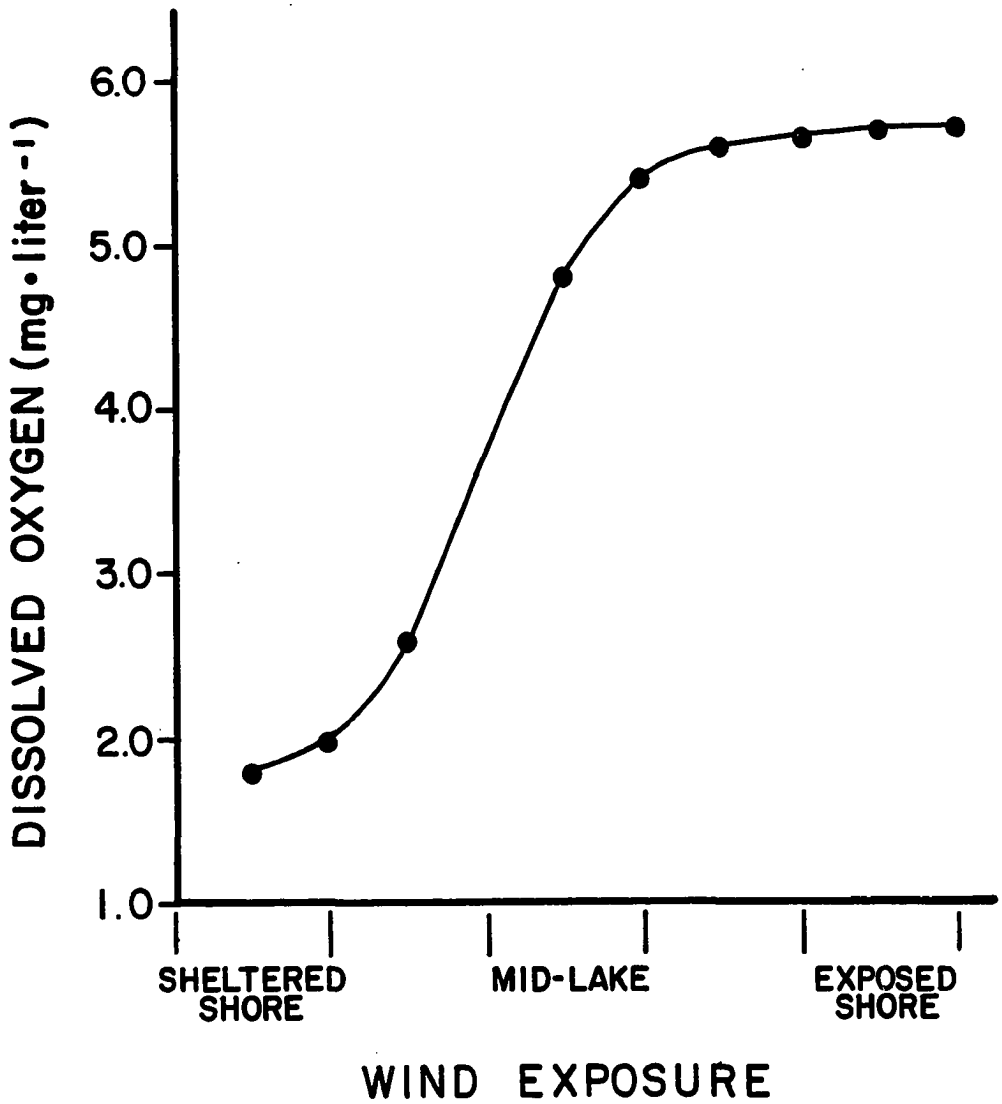

Figure 11. Effect of wind exposure on dissolved oxygen levels in Lake 10, Scottie-Desper Creeks Study Area, Alaska; 1980. Data collected at 1.0 m depth every 30 seconds along a single transect oriented with the wind direction (water temperatures were 18-19°C).

DISCUSSION

FLUVIAL INFLUENCES

Although the nature and degree of influence that hydrology exerts on lake productivity could not be directly quantified, it is apparent that watershed and basin morphology strongly influences lake processes in the Scottie-Desper Creeks Study Area. Undoubtedly, connected lakes are affected by fluvial influences to a greater degree than isolated lakes. The degree of hydrological interchange of a lake with Scottie Creek would effect budgets of dissolved and transported materials such as carbon and nutrients. Odum and Prentki (1978) identified the fluvial pathway as one of three major pathways by which allochthonous carbon could be transported into lakes (in addition to litter and precipitation). Because all lakes were roughly ellipsoid in shape, differential effects of litter and precipitation would largely depend on lake size and/or drainage area of the lake. Because lake types in Figure 6 broadly overlapped in size (Component II) but segregated according to the nature of hydrological association with the creek, the limnological differences between lake types depicted in Figures 6 and 7 and Table 1 may be largely due to fluvial effects.

Flux rates of dissolved nutrients, nutrients complexed with humic compounds and nutrients "packaged" as bacteria/detritus associations are undoubtedly important in regulating and modifying lake dynamics of connected lakes. However, the nature and degree of these influences are unknown.

LAKE PRODUCTIVITY

Nutrients, especially phosphorus and/or nitrogen, often act as limiting factors of primary productivity in freshwaters (e.g. Vollenweider 1968; Welch 1980). More specifically, lake productivity is regulated by the flux and cycling of nutrients (Likens and Loucks 1978). Levels of reactive phosphorus (P) and nitrate (N) in lakes from Scottie-Desper Creeks Area were generally in the same range as those reported for other interior lakes (Table 2), with connected lakes and Lakes 10 and 17 approximating the levels reported for Ace and Deuce Lakes which are relatively high according to interior Alaskan standards (Alexander and Barsdate 1974).

In addition to P and N levels, t-alkalinity (bicarbonates, carbonates, and hydroxides) has been shown to influence levels of primary productivity (Wetzel 1975). These ions provide an inorganic pool of carbon that is essential to the photosynthetic metabolism of algae and submerged macrophytes and also provide the buffering capacity of water. Connected lakes have significantly higher levels of t-alkalinity than isolated lakes (Table 1). These data suggest that higher levels of nutrients and ions may contribute to higher production in connected lakes than in isolated lakes. This interpretation is consistent with the findings of Murphy *et al.* (in press), that waterfowl density and species richness were significantly greater on connected lakes of the Scottie-Desper Creeks Study Area.

LAKES 10 AND 17: COMPARISON

Lakes 10 and 17 differed considerably in size, maximum depth, exposure to wind, and to a lesser degree, shape (Figures 4 and 5).

Lake size and shape are important in determining the relative importance of inputs of allochthonous litter from shore vegetation. Because Lake 17 is approximately 3.5 times larger in surface area than Lake 10 and has a more uniform shoreline, allochthonous riparian inputs would be relatively less important.

Perhaps the single most important difference between these two lakes involves their respective depths. For large lakes, mean depth is regarded as the single best index to lake trophic status (Wetzel 1975) and is one of two key predictors used to evaluate potential fish yields in lakes (Ryder et al. 1974). Depth influences the vertical distribution of heat and oxygen, which in turn are influenced by the timing and intensity of physical mixing by wind. Depending upon light extinction rates, basin depth limits the ratio of colonizable littoral zone for macrophytes (and associated periphyton) which can constitute a major fraction of autochthonous carbon production (Devol and Wissmar 1978). Lake 10 had a maximum depth of less than 2.0 m and was dominated by macrophytes. Conversely, Lake 17 had a substantial area less than 2.0 m deep and virtually no macrophytes. Reasons for their absence is unknown. However, based on these observations it is clear that autochthonous production of Lake 10 included a relatively larger macrophytic component than that of Lake 17.

The nature of spring thermal stratification is very dependent on prevailing wind conditions, especially in humic stained lakes where thermal absorbtion is increased (Alexander and Barsdate 1974). In such lakes it is not uncommon to observe surface temperatures of 7 or 8°C the day after ice melts (Alexander and Barsdate 1971). Although most

lakes in interior Alaska are dimictic (Alexander and Barsdate 1974), reoxygenation in spring may be prevented by lingering ice-cover (LaPerriere 1981).

Lakes 10 and 17 possessed fundamentally different vertical profiles for temperature and dissolved oxygen (Figures 8, 9 and 10). Although, the temperature profile in Lake 17 varied seasonally (Figure 8), each sampling date (except July) was characterized by a recognizable thermocline with hypolimnetic temperatures approximating 4°C (Figure 8). Although data are incomplete for spring, it is possible that spring turnover occurred prior to the first sampling date (19 June, 1979). However, in fall, the isothermal conditions in September (Figure 8) suggest that a fall turnover took place. Thus, Lake 17 is probably a dimictic lake.

In contrast, Lake 10 generally exhibited uniform thermal profiles and probably underwent thorough mixing to the bottom at several times during the summer. This notion is supported by the uniform thermal gradients and the temporal and spatial patterns in dissolved oxygen concentrations (Figure 10). It seems that exposure to local wind conditions was more important in regulating oxygen conditions (Figures 10 and 11) than either diel or seasonal factors.

In Lake 17, there was a persistent bloom of heterocystous Aphanizomenon sp.. Because the heterocystous blue-green algae are primarily responsible for N - fixation in open lake waters (Burris and Peterson 1978), it is likely that it is important in the nitrogen dynamics of this lake. Also, because the bloom underwent a dramatic collapse in early September, 1979, it is likely that it depressed

oxygen conditions (Barica 1978). Lake 10 had no significant algal bloom and no collapse was observed.

FISH STUDY

INTRODUCTION

GENERAL

Whitefish (Coregonidae) are widespread in cooler parts of the northern hemisphere (McPhail and Lindsey 1970). Because several species are of commercial value, many studies have examined life-history parameters that directly effect predictive estimates of commercial harvests. These include studies on fecundity and success of year classes (Lawler 1965; Hoagman 1973; Healey 1978), age and growth (Edsal 1960; Healey 1980; Mills and Beamish 1980) and population dynamics of exploited and unexploited stocks (Ayles 1976; Bell et al. 1977; Healey 1980; Imhof et al. 1980). Unfortunately, due to unresolved questions regarding taxonomy, these studies and others on general life-histories (Lindroth 1957; Lindstrom 1962; Bruce and Parsons 1979) are of limited value when species-specific information is required.

TAXONOMY

Although many taxonomic questions remain, reasons for the confusion are becoming better understood. As a group, whitefish are highly subject to morphological variation due to environmental conditions (McPhail and Lindsey 1970) and to the species composition of the surrounding fish community (Lindsey 1981). Also, there is a lack of correspondence in nomenclature between geographic areas where the same species may occur (North America, Europe, U.S.S.R.).

McPhail and Lindsey (1970) suggest that difficulties in taxonomy of whitefish are related to their evolutionary history during recent glaciation periods. They suggest that with periodic advancements of glaciers, populations of whitefish became isolated and underwent various degrees of genetic modification. Then, as the glaciers receded, whitefish populations were able to mix, resulting in some populations remaining as species and others hybridizing to form the vast array of confusing forms evident today.

In recognition of the problem of morphological plasticity, whitefish taxonomists have considered less traditional approaches for taxonomic identifications, such as electrophoresis and immunological methods (Tsuyuki et al. 1966; Chellevold 1970; Franzin and Clayton 1977; Imhof et al. 1980), as well as mineral analysis of scales (Moreau and Barbeau 1979). Although these techniques show promise, universal application does not appear imminent at the species level, due to problems associated with protein polymorphisms within a species, restricted geographic application and costs prohibitive to routine use.

At present, leading taxonomists consider the use of gill-raker counts to be the single most useful character to distinguish between closely related whitefish species (Svardson 1965; McPhail and Lindsey 1970). Although gill-raker counts have proven to be a relatively reliable taxonomic character, adaptive radiation (when other species are absent) or character displacement (when other species are present) complicates their use (Lindsey 1981).

FOOD HABITS

An underlying assumption pervading the food-habits literature of whitefish is that competition for food stringently regulates the selection for gill-raker morphology. However, the role of gill-rakers in feeding behavior of whitefish remains unclear. Many authors agree that fish with gill-rakers that are fewer in number, shorter and further apart feed mainly on benthic organisms, while fish with more, longer and closely-spaced gill-rakers feed on smaller pelagic organisms (e.g. Svardson 1952; Nilsson 1958; Lindsey 1963; Bodaly 1979). However, this generalization is not without exceptions (see Kliewer 1970).

Of particular significance to this study are the studies on lakes in Yukon Territory, Canada involving lake whitefish, Coregonus clupeaformis. Much of the variation in gill-raker counts of C. clupeaformis in that region seems to be attributable to the presence or absence of planktivorous ciscoes (Lindsey 1981). In lakes which contained populations of C. clupeaformis with unimodal gill-raker counts, modes showed a marked tendency to be lower if ciscoes were present than if they were absent. Alternatively, in the few lakes where ciscoes were absent, two distinct sympatric forms of lake whitefish were found and exhibited divergent food habits (Lindsey 1963; Bodaly 1979). The forms corresponded to C. pidschian and C. clupeaformis of McPhail and Lindsey (1970) and they partitioned the food resource such that C. pidschian was the primary benthic forager (gill-raker mode = 23) and C. clupeaformis (mode = 28), the planktivore.

OBJECTIVES

This study investigated the summer feeding habits of a form of humpback whitefish of the genus Coregonus. Its taxonomic status remains uncertain due to confusion in the literature. In the Canadian literature, it corresponds to the low gill-raker count form of C. clupeaformis (e.g. Lindsey 1963; Bodaly 1979). But in Alaska, Alt (1979) referred to this form as C. pidschian of the "C. clupeaformis" complex of McPhail and Lindsey (1970). For convenience here, the names C. pidschian and "low rakered form" are used interchangeably.

With the exception of Alt (1979), little has been published on the biology of C. pidschian in Alaska. Alt summarized a diffuse body of data collected by the Alaska Department of Fish and Game between 1967 and 1977. His primary syntheses included sections on distribution, spawning, regional age and growth patterns and usage of whitefish by Alaskan residents. However, little is known about the feeding ecology of C. pidschian.

The specific objectives of this study were designed to compliment an investigation of the benthic macroinvertebrate community of Lake 17, a small lake in the lower Scottie-Desper Creeks Area. The objectives were to:

1) determine which fish species numerically dominate the system,
2) evaluate the food habits of all dominate fish species according to size classes and
3) compare diets between sexes, seasons (spring/fall), depths and times of day within each size class of each species.

Not all pairwise comparisons of objective three were made due to time constraints and limits on fish collection permit quotas.

Although this study was not designed to accommodate questions pertaining to taxonomy and morphological plasticity of whitefish, the unexpected discovery that C. pidschian was the only fish species present in substantial numbers afforded an opportunity to study its feeding behavior and associated gill-raker counts in the absence of competitors.

METHODS

FIELD

Fish samples were obtained during spring (19 June) and fall (26 and 27 August) of 1980. Because species composition and size structure of the fish community were unknown, gill nets and minnow traps were selected for use to ensure capture of individuals of all species and sizes. All gill nets were of sinking design, made of green monofiliment nylon and were 1.8 m (6 ft) deep. In spring, several nets of a variety of lengths were fished in deep (1.4-2.5 m) and shallow (0.0-1.0 m) water. The offshore end of the gill net was weighted to ensure capture of fish near the bottom at arbitrarily selected sites. The stretch mesh of panels varied from 2.5 to 12.7 cm (1 to 5 in). Five minnow traps were baited with salmon eggs and/or bread and were fished for a continuous period of 48 hours along a depth gradient including deep and shallow zones.

In fall, methods were altered. Instead of collecting fish in deep and shallow zones, fish were captured at a single net location in shallow water (same location as in spring) during four periods of the light cycle (0400-0500 h, 0800-0900 h, 1100-1200 h, 1700-1800 h). Minnow traps were fished as in spring.

Species identifications, sex, total lengths and weights of fish were determined in the field (fork and total lengths in spring). Intact stomachs inclusive of esophagus and pylorus were removed and preserved in 10% formalin within one half to three hours following fish capture.

LABORATORY

All contents anterior to the pyloric sphincter were removed and transferred to 80% ethyl alcohol. Only recognizable food items were considered because fish swallowed items without chewing and contained relatively small amounts of detritus at all times. All non-zooplankters were initially counted. If there appeared to be more than an estimated 2000-3000 zooplankters, contents were gently teased apart and subsampled with a Henson - Stemple pipette. Intact chironomidae larvae and chironomid heads were identified and counted separately because residence times in the gut are likely to differ.

Enumerating and estimating volumes for dipteran pupae was complicated by their fragmentation in guts. Bodies were usually headless, and often broken. Therefore, numbers of pupae were obtained by counting pupal heads (attached or unattached to bodies). Intact pupae were used to estimate an average volume per pupae, then volumes were estimated by expanding for total numbers found in each gut.

Volumetric determinations were made according to a modified Hynes Point method (Hynes 1950). The modification involved use of smaller volumetric units. Separate taxa were allowed to settle overnight in 4 dram vials. Then, a simple scale with arbitrary units (4 mm increments) was placed behind each vial and volumes were read directly. Samples with large nematodes were lightly compressed to minimize spaces between organisms. Degree of compression was regulated by eye, depending upon the condition of individual samples. Gut-fullness was computed by summing the volumes of all taxa in a single gut. This was reasonable because all fish were of comparable size and could therefore be assumed to have similar gut capacities.

Age and gill-raker number were determined for six fish obtained in fall. Scales were cleaned with a test-tube brush, moistened, placed between two 20 mil acetate slides and pressed with a Carver scale press (Model C). Scales were pressed at 8.8 mt (20,000 lbs.). Scale images were magnified and read by two individuals on a portable micro-fiche reader (Bell and Howell "Commuter" Model).

STATISTICAL ANALYSES

Analysis of variance (ANOVA) was the statistical model selected to evaluate food habits (Dixon and Brown 1979: BMDP 7D). The underlying assumptions of a fixed effects model are additivity of effects of treatment, normality and independence of error and equality of group variances. The greatest problem in violating the assumptions occurs with unequal variances in the presence of unequal sample sizes (Zar 1974). When this occurs, the probability of a Type I error will depart from alpha, depending upon the magnitude of the heterogenity.

Problems with normality and unequal variance with unequal cell sizes were encountered. Therefore a logarithmic transformation was performed to correct for heteroscedasticity. Levene's test for unequal variances revealed that heteroscedasticity was not corrected for some taxa. However, since most significant differences were very high ($P < 0.01$ and $P < 0.001$) it is unlikely that unequal variances would seriously alter any conclusions made in this study.

RESULTS

POPULATION CHARACTERISTICS

In 1980, three species of fish were captured with gill nets from Lake 17. Of 126 fish netted, 124 were humpback whitefish (C. pidschian), one was a longnose sucker (Catastomus catastomus) and one was a northern pike (Esox lucius). No fry or juveniles of any species were captured.

The entire whitefish population apparently consisted of fish that were reproductively mature. Alt (1979) reported that humpback whitefish generally reach maturity at 310-360 mm fork length, corresponding to ages IV-VI. Based on age/length distributions of humpback whitefish from three interior rivers in the upper Yukon River drainage (Alt 1979), fish from this study corresponded to fish of age V or older. Over 70% corresponded to age class VI, with fork lengths between 363 and 394 mm.

Gill-raker counts of fish in this study were also similar to those reported by Alt (1979) from other interior Yukon locations (Table 4). Although the sample sizes are small and the variation in numbers of gill-rakers is relatively large for a given location, the mean and modal gill-raker numbers are relatively uniform between locations.

ANALYSES OF FOOD HABITS

Both numbers and volumes of food items were used to compare diets of humpback whitefish between sexes, depths, ($\leq$ 1.0 m vs. $>$ 1.0 m), seasons (spring vs. fall) and time of day (0400-0500 h, 0800-0900 h,

Table 4. Comparison of gill raker characteristics of populations of Coregonus pidschian from upper Yukon River drainage, Alaska 1980. Data from Alt (1979).

	Number of gill rakers				
Location	X	SD	Mode	Range	n
Chatanika R.	24.3	1.23	24	23-27	21
Chena R.	23.7	0.88	23	21-25	12
Chisana R.	23.3	1.27	23	22-25	19
Kandik R.	23.3	0.50	23	23-24	4
Porcupine R.	23.2	0.89	23	22-24	27
This study	24.2	0.90	25	23-25	6

1100-1200 h, 1700-1800 h). Tables 5 and 6 are summaries of results for the analyses and correspond to pie diagrams in Figures 12 and 13.

In general, results of number and volumetric analyses corresponded closely with each other (Tables 5 and 6). However, the results of the numerical analyses showed significant differences for more taxa than did the volumetric analyses. Differences generally involved taxa containing numbers that were small in size and not present in numbers sufficient to constitute significant volumes (e.g. Copepoda, Ostracoda and Hydracarina), or larger-sized taxa that were present in either very low or high numbers in only a few guts (e.g. Corixidae, Ceratopogonidae, Amphipoda and Gastropoda); (compare Table 6 with Figures 12 and 13).

In both numerical and volumetric analyses, most differences were highly significant ($P < 0.001$ or $P < 0.01$). In comparisons between depths, seasons and time of day, significant differences occurred in both numerical and volumetric analyses for Cladocera and Chironomidae. These two groups comprised the bulk of the diet in all comparisons (Figures 12 and 13).

There were no significant differences for any food types between male and female fish (Table 5). In contrast to the uniformity in diet between the sexes, diet composition changed radically between fish captured at different depths (Figure 12B). Differences in biovolumes were highly significant for most food types (Table 5). This change in diet is ecologically significant, because it demonstrates a shift from a more benthic diet in the shallows, to a planktivorous diet in deeper water.

Table 5. Summary of analyses of variance based upon biovolumes of prey items present in guts of Coregonus pidschian from Lake 17, Scottie-Desper Creeks Study Area, Alaska, 1980. Analyses performed on $\log_{10}$ transformed data. Depth comparison is $\geq$ 1.0 m versus < 1.0 m; seasonal comparison is spring (19 June) versus fall (26 and 27 August); times of day comparison is 0500 h versus 0800 h versus 1200 h versus 1800 h.

	Significance Level		
Comparison	0.001	0.01	0.05
Sexes	--	--	--
Depths	Cladocera	Nematoda	Sphaeriidae
	Chironomidae	--	--
	Chaoboridae	--	--
Seasons	Chaoboridae	Sphaeriidae	Chironomidae
Times of day	Cladocera	Chironomidae	--

Table 6. Summary of analyses of variance based upon numbers of prey items present in guts of Coregonus pidschian from Lake 17, Scottie-Desper Creeks Study Area, Alaska, 1980. Analyses performed on $\log_{10}$-transformed data for all taxa except Nematoda. Depth comparison is $\geq$ 1.0 m versus < 1.0 m; seasonal comparison is spring (19 June) versus fall (26 and 27 August); times of day comparison is 0500 h versus 0800 h versus 1200 h versus 1800 h.

	Significance Level		
Comparison	0.001	0.01	0.05
Sexes	--	--	Amphipoda
Depths	Cladocera	--	--
	Chironomidae	--	--
	Chaoboridae	--	--
	Gastropoda	--	--
	Ostracoda	--	--
Seasons	Cladocera	Gastropoda	Chironomidae
	Chaoboridae	Ceratopogonidae	--
	Ostracoda	--	--
	Hydracarina	--	--
Times of day	Cladocera	Sphaeriidae	Corixidae
	Chironomidae	Hydracarina	Copepoda

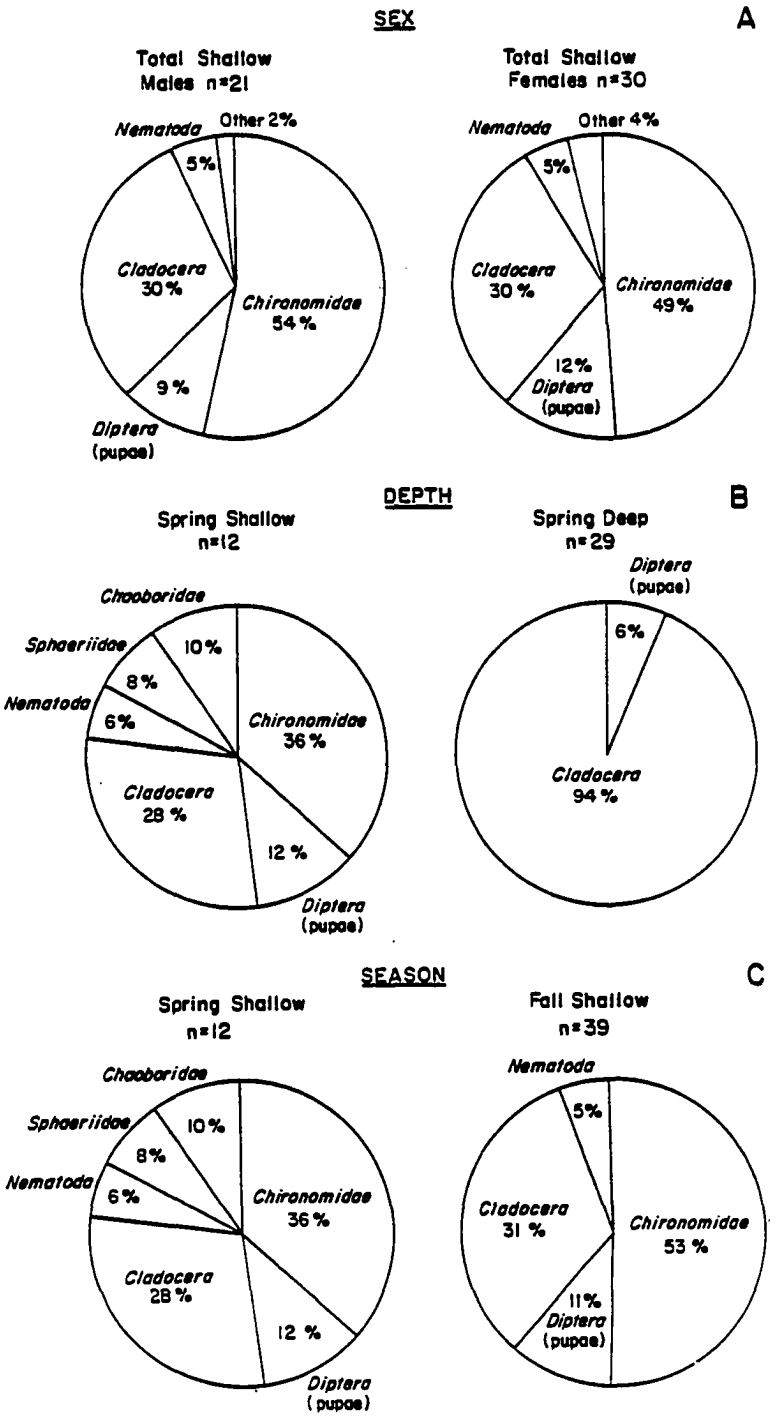

Figure 12. Comparison of diet of Coregonus pidschian between sexes, water depths and seasons. Percentages computed from biovolumes; deep and shallow strata refer to water depths > 1.0 m and depths ≥ 1.0 m, respectively; spring and fall refer to 19 June and 26 and 27 August, 1980, respectively: Scottie-Desper Creeks Study Area, Alaska.

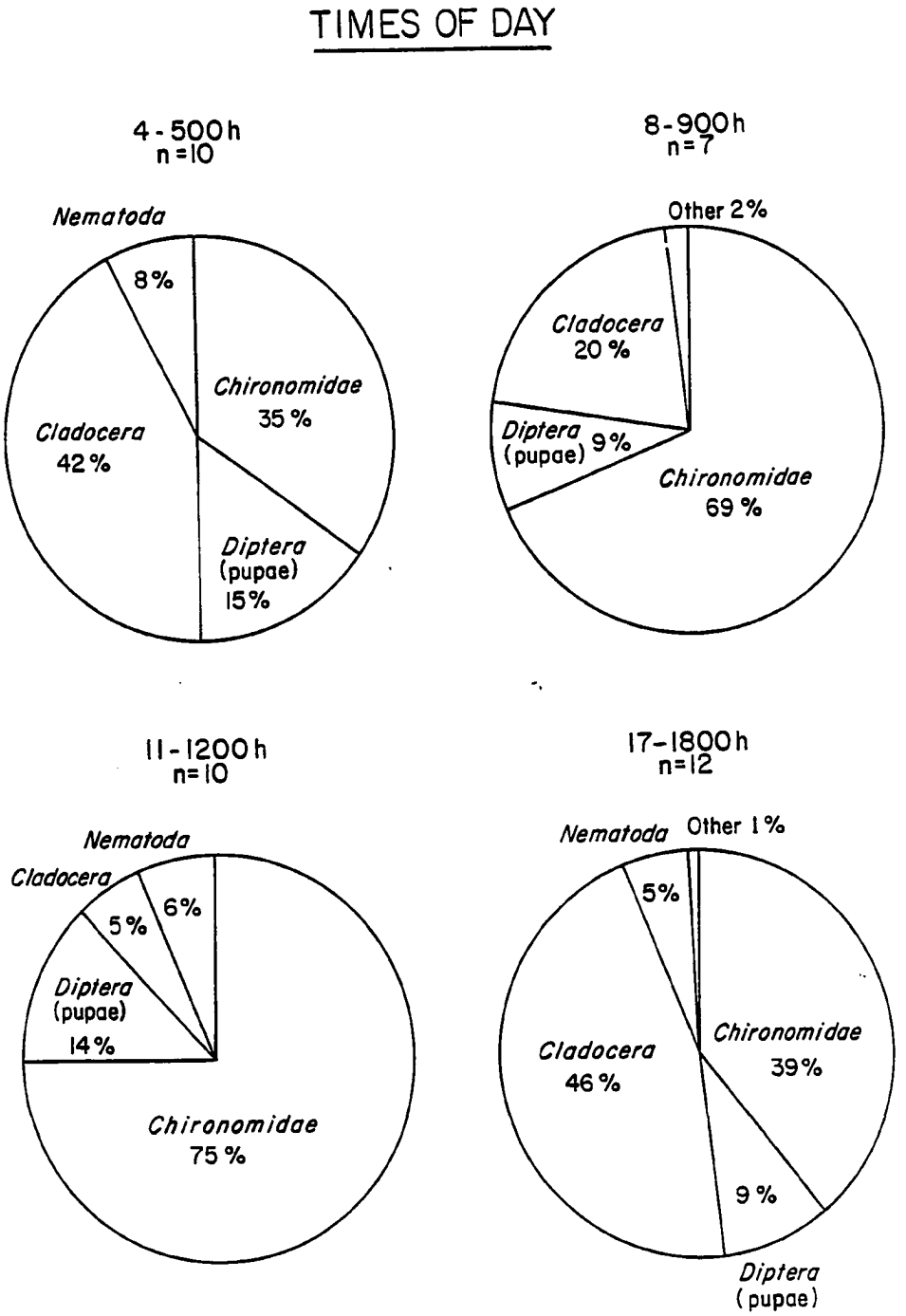

Figure 13. Comparison of diet between times of day for Coregonus pidschian. Percentages computed from biovolumes. All data from 26 and 27 August, 1980, Scottie-Desper Creeks Study Area, Alaska.

The comparison between spring and fall diets in Figure 12C revealed two basic differences. In fall, the groups Sphaeriidae and Chaoboridae were entirely absent and thus were significantly different when compared to spring (Table 5). Secondly, the volumes of chironomids and cladocerans were significantly greater in fall than spring (Table 5). In fall, the composition of diet was compared at four times during the light cycle (Figure 13), with time designations representing approximate times of fish capture. The relative proportions of chironomids and cladocerans changed radically at different times of day, but collectively represented over 75% of the diet at each time period. Proportions and volumes of nematodes and pupae remained relatively constant and were not significantly different (for volumes) at different times of the day (Table 5).

The percentages of the diet represented by cladocerans and chironomids were inversely related (Figure 13). The proportion of cladocerans decreased from 42% in early morning to a low of 5% at noon and then increased again to 46% by early evening. Conversely, chironomids increased from 35% in early morning to 75% at noon and then decreased again to 39% by early evening. This same pattern occurred for volumes of food type in the gut (Figure 14B). As the volume of chironomids in the gut increased from morning to noon, there was a corresponding decrease in the volume of cladocerans consumed over the same period.

This inverse relationship is most pronounced between the noon and early evening. Cladoceran volume increased sharply, while the volume of chironomids decreased, resulting in slightly greater volumes of cladocerans in the guts by evening. Total gut-fullness increased to

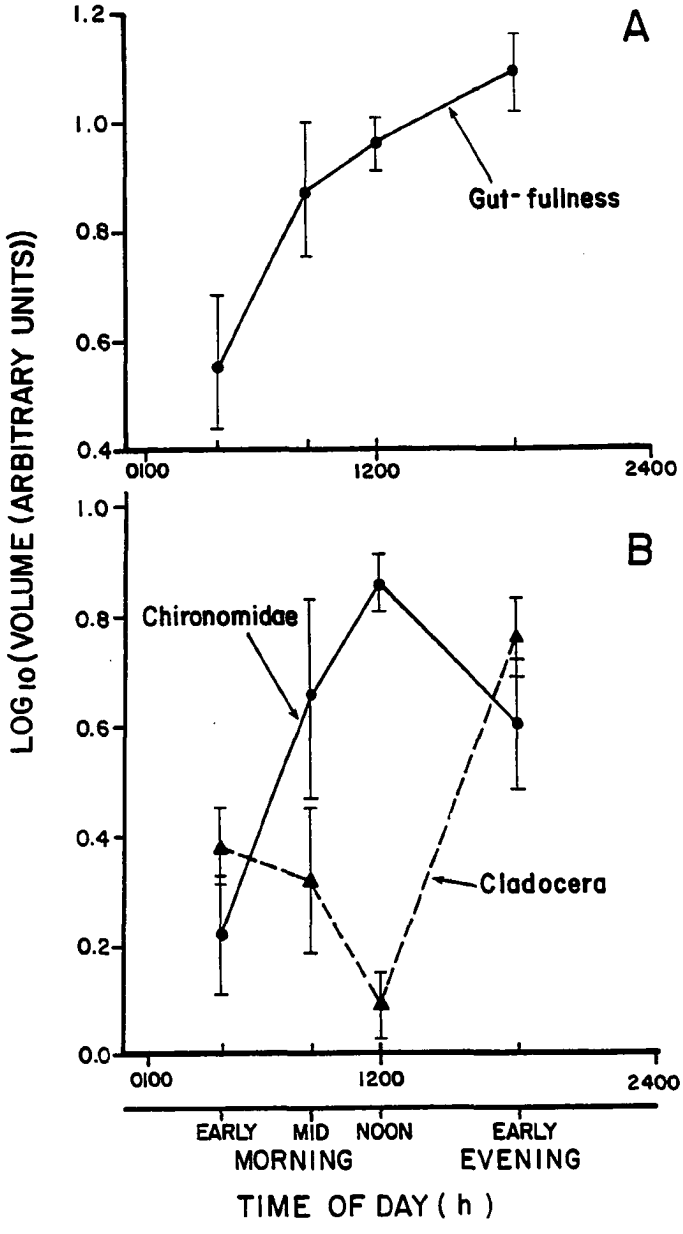

Figure 14. Diel pattern of gut-fullness and consumption of Chironomidae and Cladocera for Coregonus pidschian. Data collected on 26 and 27 August, 1980, Scottie-Desper Creeks Study Area, Alaska. Points are means ±SE; (n=10 at 0500 h and 1200 h; n=7 at 0800 h; and n=12 at 1800 h).

its highest recorded level at 1700-1800 h (Figure 14A). Although gut-fullness was lowest in early morning (Figure 14A), the proportions of food items were similar for morning and evening sampling periods (Figure 13).

DISCUSSION

COMPARISONS OF FOOD HABITS

Humpback whitefish (C. pidschian), was the only species of fish captured in significant numbers in Lake 17. For the subsample of fish examined, all were age V or older. Seasonal use of the lake appeared consistent with the general pattern described by Alt (1979). Apparently, fish migrate into lakes following spring ice-melt, feed during the summer and then emigrate to spawn or overwinter in fall. The fact that no juvenile fish of any species were captured supports the notion that this lake experiences periods of anoxia in winter and may explain the striking simplicity of the fish community.

Figures 12 and 13 show that chironomids and/or cladocerans collectively comprised the bulk of the diet by volume. However, the relative importance of each changed significantly between depths, seasons and times of day (Table 5). It is surprising that these two groups consistently comprised the bulk of the diet since they were radically different in size and are generally spatially segregated in aquatic habitats.

Cladocerans were approximately 2 - 3 mm in length, whereas chironomids generally ranged from 15 - 25 mm. Also, the consistency in diet between spring and fall is remarkable, since zooplankton are subject to extreme seasonal fluctuations in numbers due to environmental factors (Porter 1977).

Chironomids are benthic organisms and cladocerans are planktonic. Thus, large shifts in diet between these two groups suggests that fish must be able to change searching methods and habitats since fish may

only use one search method at a time when foraging for food (Crow 1976). Murdoch et al. (1975) hypothesized that fish may feed in one area but leave occasionally to sample another area, comparing reward rates and staying longer in the more rewarding area. Optimal foraging theory (Schoener 1971; Werner and Hall 1974; Eggers 1977) predicts that the predator will switch to alternative prey types as the relative abundance and size of available prey, or ability of the predator to exploit available prey changes (Eggers 1977). Because fish preferentially forage on larger prey species (Zaret 1980), the dramatic increase in relative importance of cladocerans in the deeper water zone (Figure 12B) and between noon and 1800 h in Figure 13, represents an unlikely event unless relative "available" abundance of prey and/or ability of the predator to capture various prey changes.

The simplest explanation in keeping with optimal foraging theory is that the ability of whitefish to capture chironomids decreased with depth. This may be due to the attenuation of light below the visual threshold of the fish since the water is stained brown. Such thresholds have been shown to exist in theory (Eggers 1977) and in feeding experiments (Brett and Groot 1963).

In contrast to Figure 12B, which represents fish captured in two depth strata at one time, Figure 13 represents fish captured in one depth stratum (0.0 - 1.0 m) at different times of day. Undoubtedly, visual acquity of whitefish would change over a 24 hour cycle as light conditions changed causing relative "availabilities" of chironomids and cladocerans to likewise change. However, the phenomenon of vertical migration (Hutchinson 1967; Vol. II) by zooplankton could also account for dramatic changes in the "availability" of cladocerans.

Most planktivorous fish are visual predators (Werner and Hall 1974), and are restricted to foraging when light conditions are adequate. Many, if not most, zooplankton species interrupt foraging to migrate into deeper water during the day and then return to the surface to feed as light conditions wane in afternoon and evening. Although causes and regulating mechanisms are not known with certainty (Kerfoot 1980) this behavior reduces exposure of zooplankton to fish predation and may result in dramatic changes in absolute and relative abundances of prey.

The relative importance of chironomids and cladocerans change reciprocally over time as shown in Figure 13. The basis for this is not known and could not be addressed in this study. However (adhering to Occam's razor), I propose a simple explanation of Figure 13, consistent with general theory regarding visual predation and optimal foraging in fishes. As light levels increased from 0400 h to 1200 h, chironomids became more visible on the bottom and were consumed in greater amounts and zooplankton migrated to the sediment, becoming much less available. At 1100-1200 h when light conditions were optimal, chironomids were consumed in much greater volumes than cladocerans. As light levels waned by evening, visibility of chironomids became reduced and cladocerans returned to the surface and were consumed in much greater quantities (1700-1800 h).

BEHAVIORAL IMPLICATIONS

In Yukon Territories, Canada, sympatric forms of lake whitefish C. clupeaformis partitioned the available food resource such that the low-rakered forms (gill-raker mode = 23), (corresponding to C. pidschian) consumed primarily benthic prey and the high-rakered form (mode = 28) primarily consumed zooplankton (Lindsey 1963, Bodaly 1979). Humpback whitefish (C. pidschian), obtained in this study, consumed large proportions of both benthic and zooplankton prey and had an intermediate modal count of 25 (Table 4).

Much effort has been spent attempting to determine the role of gill-raker morphology in whitefish and food habits. Kliewer (1970) suggests that gill-raker characteristics do not necessarily play a significant role in influencing the type of food eaten, but rather the method (mode) of feeding (i.e. capture of individual prey or gulping of many prey). Further, he suggests that whitefish can display two different methods of feeding, depending on whether they are eating benthic or pelagic organisms. When fish are consuming benthic organisms he suggests that fish simply "suck up" individual organisms (particulate feeding mode), whereas when fish feed on plankton, they swim with their mouths open constantly gulping (gulping feeding mode). Although the method of feeding on benthos proposed by Kliewer has not been substantiated, gulping and particulate feeding modes have been demonstrated in two closely allied ciscoe species, C. hovi and C. artedii. Although Seghers (1975) performed feeding experiments on C. clupeaformis (gill-raker range 24 - 28) he failed to demonstrate a gulping feeding mode even at relatively high prey densities.

In the present study, feeding rates, digestion rates and the timing of zooplankton vertical migration were not determined. However, if Seghers' data reflect a maximum feeding rate applicable to C. pidschian for a particulate feeding mode, results from this study suggest that a gulping feeding mode may exist under some conditions.

It is significant that gut-fullness increased from noon to 1800 h (Figure 14A) while volumes of chironomids and cladocerans underwent reciprocal trends (Figure 14B). If the volume of chironomids decreased, either by digestion or reduced consumption and gut-fullness increased, the increase is necessarily due to other food sources. Since 85% of the total volume in the guts during this time was composed of chironomids and cladocerans (Figure 13) cladocerans accounted for the majority of additional biovolume. Further, these fish must be reasonably efficient planktovores because they achieved greatest gut-fullness when guts were dominated by plankton (Figure 14, 1700-1800 h).

In spring, a few fish contained enormous numbers of cladocerans (maximum approximately 50,000 cladocerans/fish). Assuming no digestion, and a constant feeding rate, a fish would have had to consume 0.58 Cladocera per second for 24 hours in order to contain 50,000 in its gut. This rate approximates the maximum rate of 0.67 Daphnia per second reported by Seghers (1975) for C. clupeaformis. Because there are several factors that may regulate feeding activity (e.g. vertical migration of prey, gut-fullness, light conditions) and/or the observed number of prey in a gut (e.g. digestion), it is likely that the rate, 0.58 Cladocera per second, is an underestimate of the actual feeding rate.

It is clear that consumption of cladocerans was not constant at all times of day (Figures 13 and 14B). Also, because the slope of the line for Cladocera (Figure 14B), between 0900 h and 1200 h, represents the combined effects of digestion and reduced consumption over that period, it can be regarded as a conservative approximation for rate of digestion of cladocerans. From the steep slope, it can be seen that the digestion rate of cladocerans was rapid and certainly much less than 24 hours. If the maximum feeding rate reported by Seghers (1975 applies to C. pidschian the enormous numbers of zooplankton found in some fish guts suggests that either fish possess another feeding mode at high prey densities, or are extremely efficient particulate feeders.

BENTHIC INVERTEBRATE STUDY

INTRODUCTION

GENERAL

This study involves the description of benthic macroinvertebrate communities of two subarctic lakes. The composition of each community of macroinvertebrates is compared by major taxa and by functional feeding groups, a method commonly used in lotic ecology (Cummins 1974).

At present there is no general conceptual model of lake ecosystem structure and function. Traditionally, researchers have devised various classification schemes in an attempt to reduce masses of descriptive information to fit logical "trophic" models (see Brinkhurst 1974). The majority of schemes have used various subsets of physical, chemical and/or biological variables to classify lake "trophy" along a gradient from "oligotrophic" to "eutrophic." Although various schemes may adequately classify lakes within a geographic area or over the "trophic range" where it was devised, none appear to be universally applicable to lakes over broad geographic or trophic ranges.

In the last decade, research centered on macrobenthos of streams has greatly expanded knowledge involving relationships between physical structure of streams and the resultant macroinvertebrate community. The "River Continuim Hypothesis" (Vannotte et al. 1980) suggests that the proportional balance between terrestrially linked heterotrphy and channel-based autotrophy strongly influences broad-scale differences in

invertebrate community structure. As the source of available energy changes from terrestrial sources to channel-based production, there are predictable changes in the morpho-behavioral adaptations of invertebrates necessary to process the changing food base (Cummins and Klug 1979).

In recognition of these morpho-behavioral changes, stream invertebrates have been classified into functional feeding groups according to adaptations for food acquisition, rather than food eaten (e.g. Merritt and Cummins 1978, Cummins and Klug 1979).

The six major functional groups recognized are briefly summarized as follows (from Cummins and Klug 1979):

1) shredders: organisms that chew, bore or mine living or decomposing vascular plant tissue;

2) collectors: organisms that primarily consume fine particulate organic matter (FPOM) by filtering or gathering techniques;

3) scrapers: organisms that graze surfaces (mineral, organic or macrophytes) for attached algae by scraping;

4) piercers: carnivores that pierce tissues and cells and suck fluids;

5) engulfers: carnivores that engulf other animals whole or in part;

6) parasites: heterotrophs that derive sustenance from a living animal host in ways other than mentioned above.

Terms used in this study generally follow those used by Cummins and Klug (1979) with the following exceptions. Collectors were partitioned into two groups, based on types of particles found in the guts; collector-gatherers of particulate organic matter (POM) and collector-gatherers of algae. Also, piercer and engulfer carnivores were denoted as piercer-predators and engulfer-predators, respectively.

In this study, the concept of functional feeding groups has been applied to communities of benthic macroinvertebrates in lakes. A goal of this study was to evaluate the appropriateness of applying a "functional feeding group" classification scheme, developed for temperate streams, to benthic macroinvertebrate communities of two subarctic lakes. The two lakes were selected for study because they differed substantially in amounts of submergent and emergent macrovegetation. This basic difference originally formed the basis for simple hypotheses regarding structural and functional properties of communities of macroinvertebrates inhabiting each lake. However, it was later discovered that fish were absent in Lake 10 and that an apparently dense population of humpback whitefish were present in Lake 17. Thus, lakes differed simultaneously in two fundamental ways; in relative importance of macrophytes as an autochthonous carbon source and in relative importance of fish predation. It was anticipated that the presence/absence of these factors would substantially affect the community structure of macroinvertebrates inhabiting each lake.

INVERTEBRATE/MACROPHYTE RELATIONSHIPS

Macrophytes effect the structure and function of aquatic systems in a variety of ways. Although they may act as nutrient pumps for sediment-bound phosphorus (Carignan and Kalff 1979; Barko and Smart 1980; Carignan 1982) and as sources of dissolved carbon (Sondergaard 1981) they are most directly used by invertebrates as sources of food and/or shelter. During the growing season relatively few invertebrates directly consume macrophytes (Soszka 1975; Urban 1975; Otto and Svensson 1981). Instead, because plant surfaces are always coated with epiphytes (Cattaneo and Kalff 1980), they are grazed by a variety of herbivorous invertebrates (e.g. Soszka 1975). For some groups, such as Odonata, macrophytes provide the structural setting for hunting prey (Merritt and Cummins 1978) as well as concealment from predators and oviposition of eggs (Walker 1953). Finally, at the end of the growing season, macrophytes become senescent and may provide at least half the total organic carbon inputs to lakes (Godshalk and Wetzel 1978).

Scenescent macrophytes rapidly become colonized by microorganisms (e.g. Wetzel 1975) which initiate the degradation process. As a result of initial microbial colonization the quality of the macrophyte as food is improved for subsequent processing by larger benthic macroinvertebrates (shredders) which shred material into "bite-sized" pieces that can be ingested (Cummins and Klug 1979). Therefore, because Lake 10 contained abundant macrophytes and Lake 17 did not, it was anticipated that the benthic macroinvertebrate community would

reflect this difference, particularly in terms of presence/absence of shredder organisms.

FISH/INVERTEBRATE RELATIONSHIPS

Research involving fish/invertebrate relationships has undergone intensive and diversified investigation following the seminal paper of Brooks and Dodson (1965) which proposed that planktivorous fish preferentially remove the largest prey from the environment. Fish selectivity has since been shown to be affected by a combination of factors, such as the fish's visual field, apparent size of prey, and encounter probabilities of predator and prey (e.g. Werner and Hall 1974; Confer and Blades 1975; O'Brien et al. 1976; Eggers 1977). In addition, species-specific abilities to escape fish predators modify effects of predation (Strickler 1975; Confer and Blades 1975) and may result in passive feeding selectivity for prey with poor escape abilities (Drenner and McComas 1980). Because fish are visual predators and preferentially remove large conspicuous prey and because invertebrate predators are generally the largest invertebrates present in lake fauna (e.g. large dytiscid beetles, dragonfly and damselfly larvae etc.), the presence of a large population of fish would be expected to negatively effect this group of invertebrates. Conversely, in the absence of fish predation, there should be relatively more large invertebrates present than if fish were present. Because Lake 10 contained no fish and Lake 17 contained humpback whitefish which consumed macroinvertebrates (see Fish Study) it was anticipated that

Lake 10 would contain relatively more large, predaceous macroinvertebrates than Lake 17.

OBJECTIVES

Specific objectives of this study were to:

1) describe and compare the communities of macroinvertebrates in two subarctic lakes in terms of numbers and biovolumes of major taxa and functional feeding groups;

2) describe and compare the taxonomic and functional feeding group composition of assemblages of macroinvertebrates that occupy near-shore (water depth $\leq$ 1.0 m) and off-shore (water depth $>$ 1.0 m) zones within each lake and compare zones between lakes;

3) test the following hypotheses related to macrophyte/invertebrate relationships:

   A. Ho: proportion of biovolume of shredders in Lake 10 = the proportion of biovolume of shredders in Lake 17;

      Ha: proportion of biovolumes of shredders in Lake 10 $\neq$ the proportion of biovolume of shredders in Lake 17;

   B. Ho: proportion of biovolume of scrapers in Lake 10 = the proportion of biovolume of scrapers in Lake 17;

      Ha: proportion of biovolume of scrapers in Lake 10 $\neq$ the proportion of biovolume of scrapers in Lake 17;

4) test the following hypothesis related to fish/invertebrate relationships:

Ho: proportion of biovolume of total invertebrate predators in Lake 10 = the proportion of biovolume of total predators in Lake 17;

Ha: proportion of biovolume of total invertebrate predators in Lake 10 ≠ the proportion of biovolume of total predators in Lake 17.

METHODS

FIELD

Following a cursory survey of 15 lakes, Lakes 10 and 17 were subjectively selected for comparative study because they possessed many observable differences in faunal and floral characteristics (see study area description). A map of each lake was constructed following Lind (1974) (Study Area: Figures 4 and 5) and invertebrates were sampled according to a stratified random design.

Three types of sampling equipment were required to adequately sample benthic and pelagic invertebrates in both lakes. In the shallow weedy stratum (depth $\leq$ 1.0 m) of both lakes, a 25 cm diameter cylinder and associated hand dip-net was used. This device sampled benthic and pelagic organisms. However, in the deeper stratum (depth > 1.0 m), each sample was composed of an Ekman grab (15 cm square) and a corresponding Wisconsin net sample (vertical tow) (9 cm diameter; 80 um mesh). The Ekman sampler captured primarily benthic organisms, whereas the Wisconsin sampler captured pelagic organisms. Five samples were obtained in each stratum of each lake during periods from 19 June - 4 July, 1979, and 29 August - 11 September, 1979, yielding a total of 40 invertebrate samples. Contents of cylinder and Ekman samples were sieved in the field (240 µm mesh) and preserved in 10% formalin. Wisconsin samples (collected with 80 µm mesh; preserved in 10% formalin) were later sieved in the laboratory through 240 µm mesh to enable comparisons to be made to samples collected with the cylinder samples.

LABORATORY

Methods for laboratory procedures are summarized in Figure 15. Environmental variables measured or derived include water depth, total amount of vegetation and wood per sample, percent organic matter of substrate and total amount of substrate per sample.

TAXONOMIC IDENTIFICATIONS, GUT ANALYSES AND BIOVOLUMES

Invertebrates were identified to taxonomic levels that allowed assignments to appropriate functional feeding groups (Appendix Table B-1). All insects were identified to the family level using Merritt and Cummins (1978). Members of Limnephilidae and Phryganeidae (Trichoptera) were later identified to generic levels using Wiggins (1977). Members of Chironomidae (Diptera) were keyed to various taxonomic levels below family by use of Merritt and Cummins (1978) and Oliver et al. (1978). Non-insect groups were identified using Pennak (1978).

For all insects greater than 5mm in length, methods for determining food types generally followed Cowen et al. (1983). Gut contents were removed, gently teased apart, and filtered with a Millipore filtering device (47 μm pore size). Filter papers containing gut contents were allowed to dry, treated with immersion oil and then mounted on microscope slides for examination. Gut contents were classed into four basic food types; algae, course particulate organic matter (CPOM = particles $\geq$ 1.0 mm), fine particulate organic matter

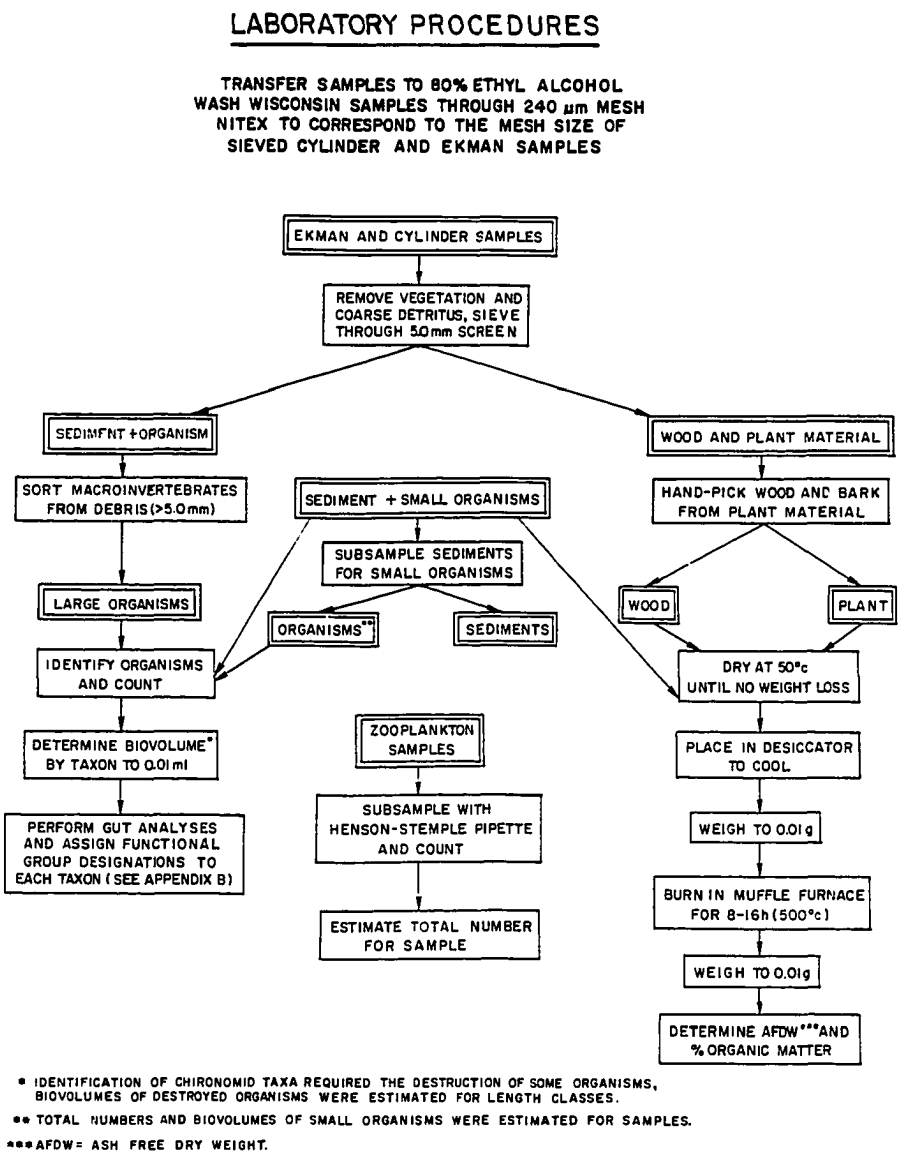

Figure 15. Methods for laboratory procedures.

(FPOM = particles < 1.0 mm) and animal material. Food types were estimated to the nearest 25% of total particle area. Results of gut-analyses are given in Appendix Tables B-3 to B-5.

Chironomids less than 5 mm in length were placed in warm 10% KOH for 5 to 15 minutes until external body tissues cleared, then placed on a microscope slide, secured with a cover slip and gut contents assessed. Functional group assignments were made on the basis of gut analyses, and/or Merritt and Cummins (1978) or Pennak (1978) (summarized in Appendix Table B-2). Because Pennak does not classify taxa according to functional feeding groups, descriptions of food-habits and feeding behaviors were used to assign non-insect taxa to feeding groups.

The device used to measure biovolumes appeared to be very precise when repeated measurements were taken on relatively large macroinvertebrates. However, its precision was less for organisms with high surface to volume ratios (e.g. ostracods and zooplankton). Therefore, a lower limit of 0.01 ml was set as the empirically-derived threshold for biovolume measurements.

STATISTICAL ANALYSES

In fall, samples were obtained in the shallow stratum of Lake 10 with both gear types (Ekman/Wisconsin and cylinder samplers) in order to compare their relative capture efficiencies. At each of five locations, both gear types were used to sample the habitat. First, a sample was collected with the cylinder sampler, followed by a one-hour resettlement period. Then, an area immediately adjacent to the first

sampling location was sampled using the Ekman/Wisconsin samplers. Comparisons of gear types were then made by adjusting numbers and biovolumes and organisms obtained with each gear type to a common volume of substrate and area of overlying water column; and then by plotting total numbers and biovolumes of benthic macroinvertebrates of each sample against depth and analyzing by inspection.

Although there appeared to be no systematic pattern of differences between numbers of organisms captured by different gear types, biovolumes of invertebrate obtained with Ekman/Wisconsin samplers were lower in each of five comparative samples. Since primary objectives did not require analysis of absolute numbers and volumes, proportions of numbers and volumes of taxa and functional groups were used.

Principal component analyses (PCA) were used to assess community structure in terms of numbers and biovolumes of taxa. Because results of PCA's on transformed (X=arcsine $\sqrt{X}$) and non-transformed data were judged to be very similar, analyses were performed on non-transformed data. Each analysis was performed on the correlation matrix.

For the PC analysis simple rules were developed to exclude taxa that were rarely encountered. For the Insecta, a family was excluded if it was not present in at least two (of ten) samples. Some odonates were damaged and/or fragmented and could not be identified to the family level. They were included if they were present in at least four samples or if they comprised 5% or more of the total volume for the ten samples. Chironomid taxa were excluded if a taxon had no measureable biovolume or if it was represented by fewer than a total of ten organisms. The list of variables included in each PC analysis for Lakes 10 and 17 are given in Appendix Table C-1.

PC analysis is a statistical method with the capability of reducing multivariate data into a few dimensions (linear combinations of the original variables) that successively account for the major independent patterns of variation in the sample (Harris 1975). Each dimension or principal component (PC) accounts for a unique and successively smaller portion of the total variance within the data set. If the original variables are highly interrelated, the first few PC's will account for a high percentage of total variation (Harris 1975).

The Mann-Whitney U test was used to compare proportion data of taxa and functional groups between: 1) strata within a given season in each lake, 2) seasons within each lake and 3) lakes for each sampling period (spring, fall) and for combined sampling periods.

Numbers and biovolumes were used for taxonomic comparisons. However, only biovolumes were used for functional group comparisons because numbers of nematodes were generally large but could not be assigned to any single functional group (biovolumes were relatively small), and numbers of oligochaetes could not be obtained because they broke into pieces during sorting and removal from the sediments.

RESULTS

DISTRIBUTION WITH DEPTH

Total numbers (excluding Oligochaeta) and biovolumes of macroinvertebrates (per sample) were plotted against depth for both sampling periods in each lake. However, due to high variability and small sample sizes (10 samples per sampling period) a clear pattern of macroinvertebrate distribution was only present for biovolume data in spring for Lakes 10 and 17 (Figures 16 and 17, respectively). Although the maximum depth in each lake was much different, biovolumes of organisms were much reduced in the deepest areas of both lakes. In Lake 10, biovolumes declined rapidly in water deeper than 1.0 m, whereas in Lake 17, the sharpest decline occurred between 4.0 - 6.0 m.

In the shallow stratum ($\leq$ 1.0 m), biovolumes were generally much reduced in Lake 17 ($<$ 0.75 ml $\cdot$ sample^{-1}), whereas in Lake 10, biovolumes exceeded 1.0 ml $\cdot$ sample^{-1} in all cases and exceeded 3.0 ml $\cdot$ sample^{-1} in two of five samples).

COMPOSITION OF LAKE COMMUNITIES

Figures 18-20 are summaries of taxonomic and functional feeding group (FFG) composition of benthic macroinvertebrate communities in Lakes 10 and 17. In Lake 10, the benthic macroinvertebrate community was dominated by Chironomidae and non-insect taxa, collectively comprising over 77% of total biovolume in spring and fall (Figure 18).

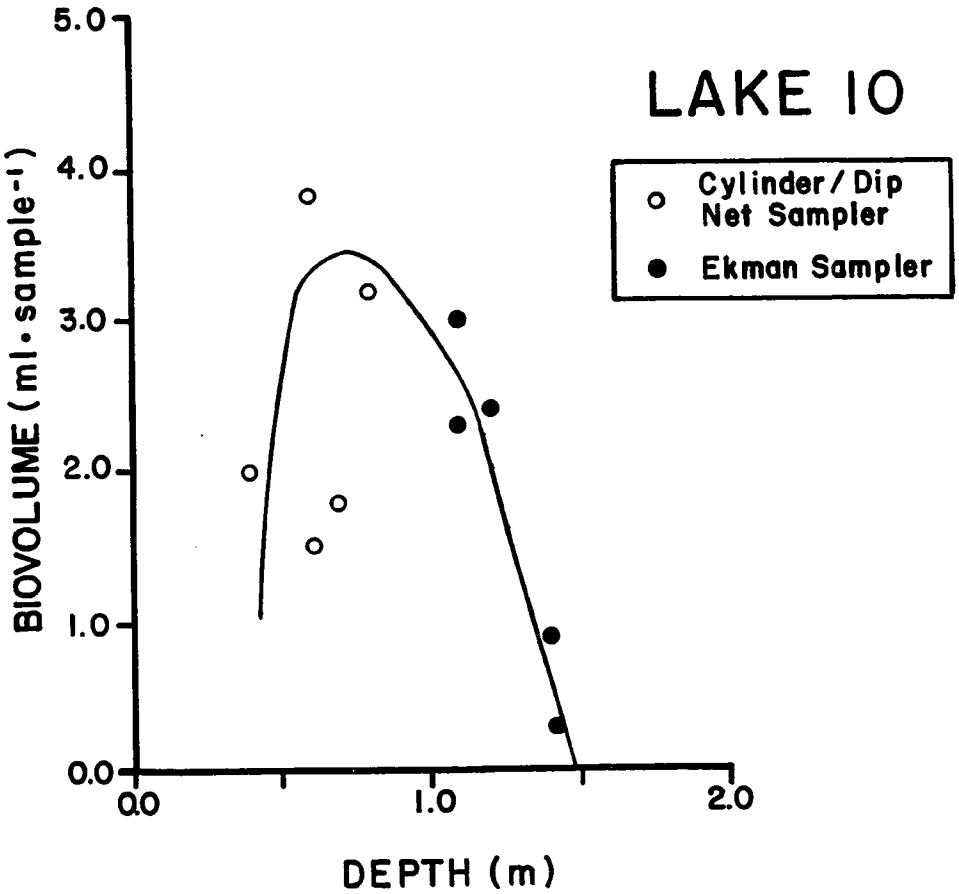

Figure 16. Depth versus total biovolume of macroinvertebrates in Lake 10, Scottie-Desper Creeks Study Area, Alaska, 1979.

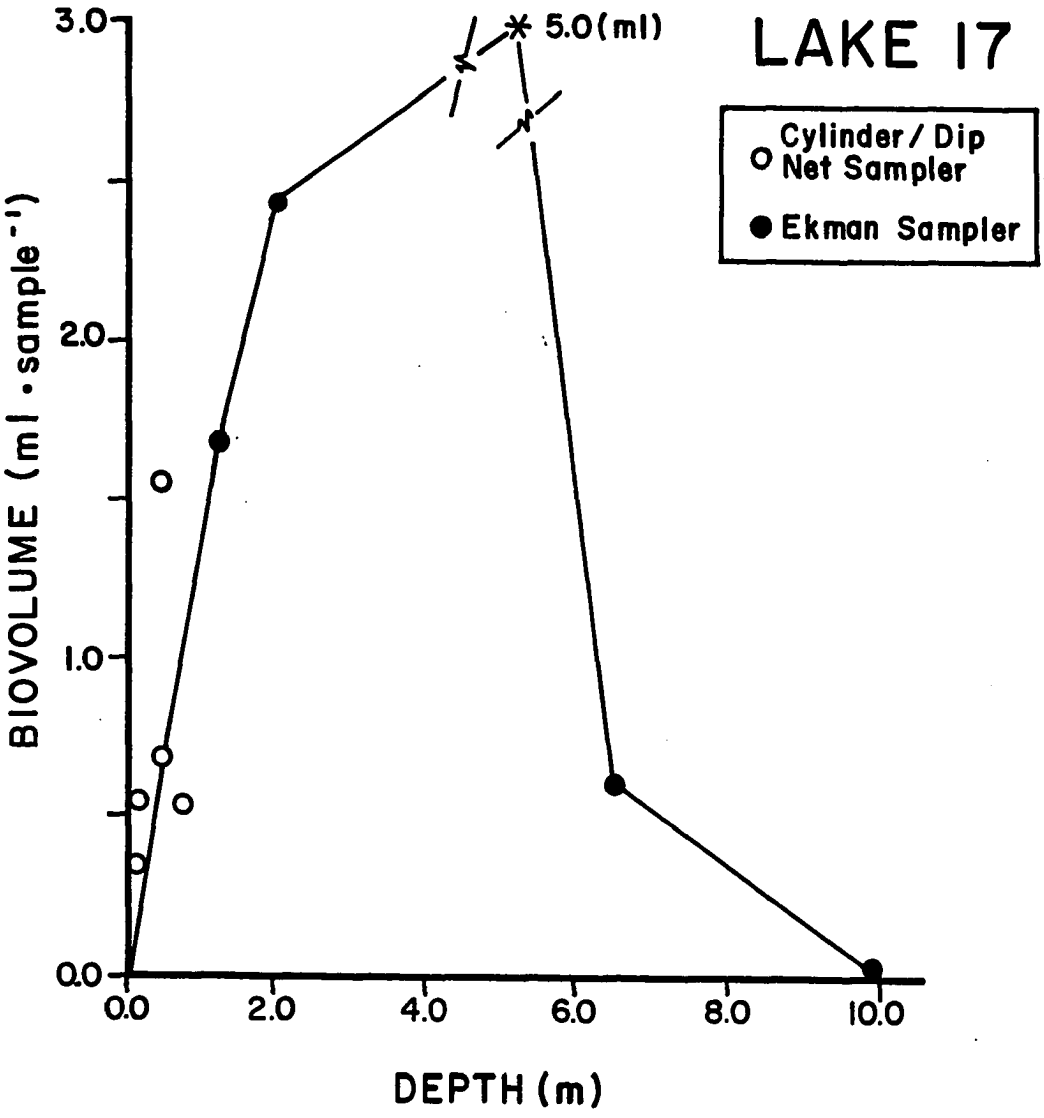

Figure 17. Depth versus total biovolume of macroinvertebrates in Lake 17, Scottie-Desper Creeks Study Area, Alaska, 1979.

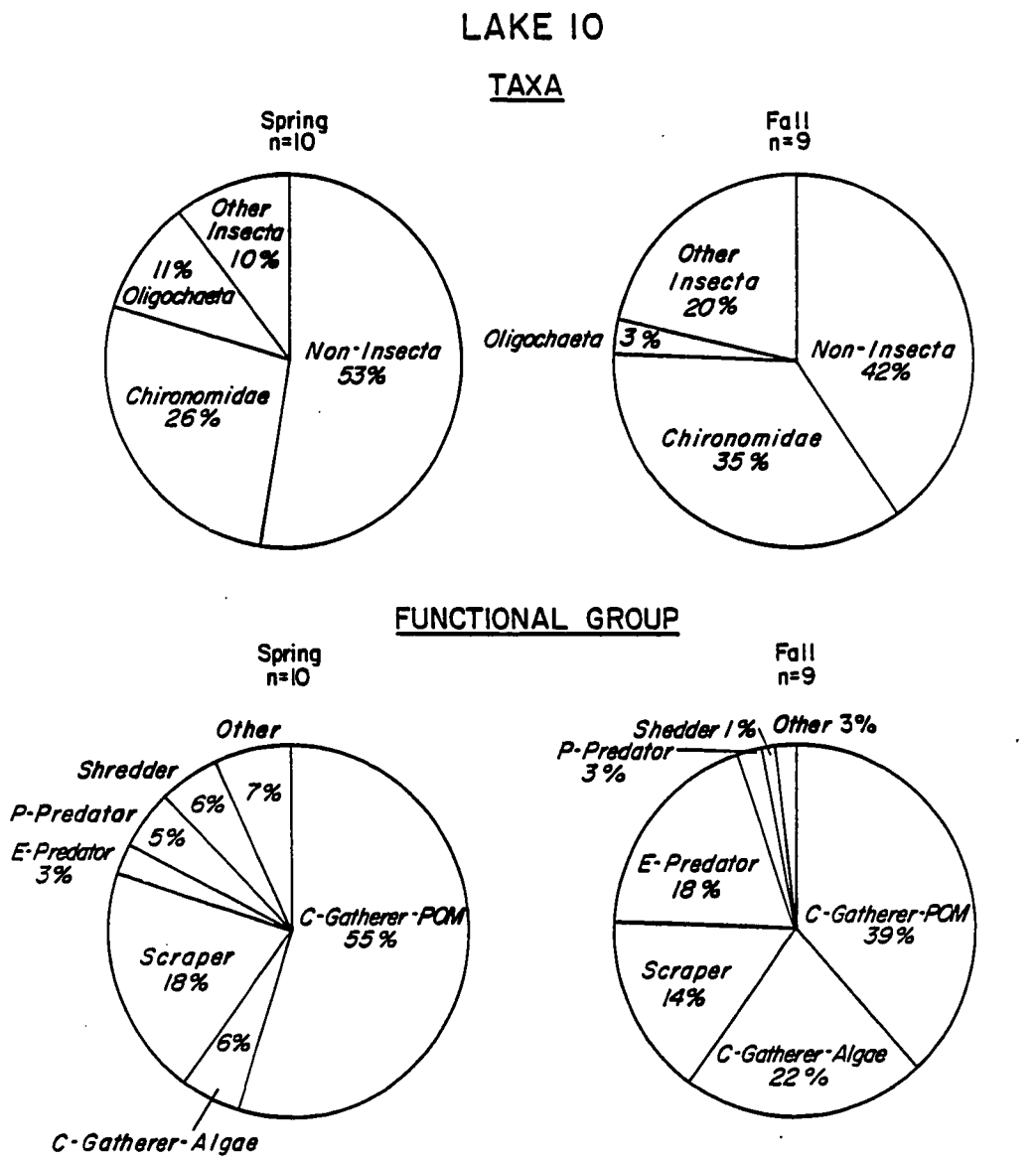

Figure 18. Summary of biovolumes of major benthic taxa and functional feeding groups present during spring (19 June - 4 July) and fall (29 August - 11 September) in Lake 10, Scottie-Desper Creeks Study Area, Alaska, 1979.

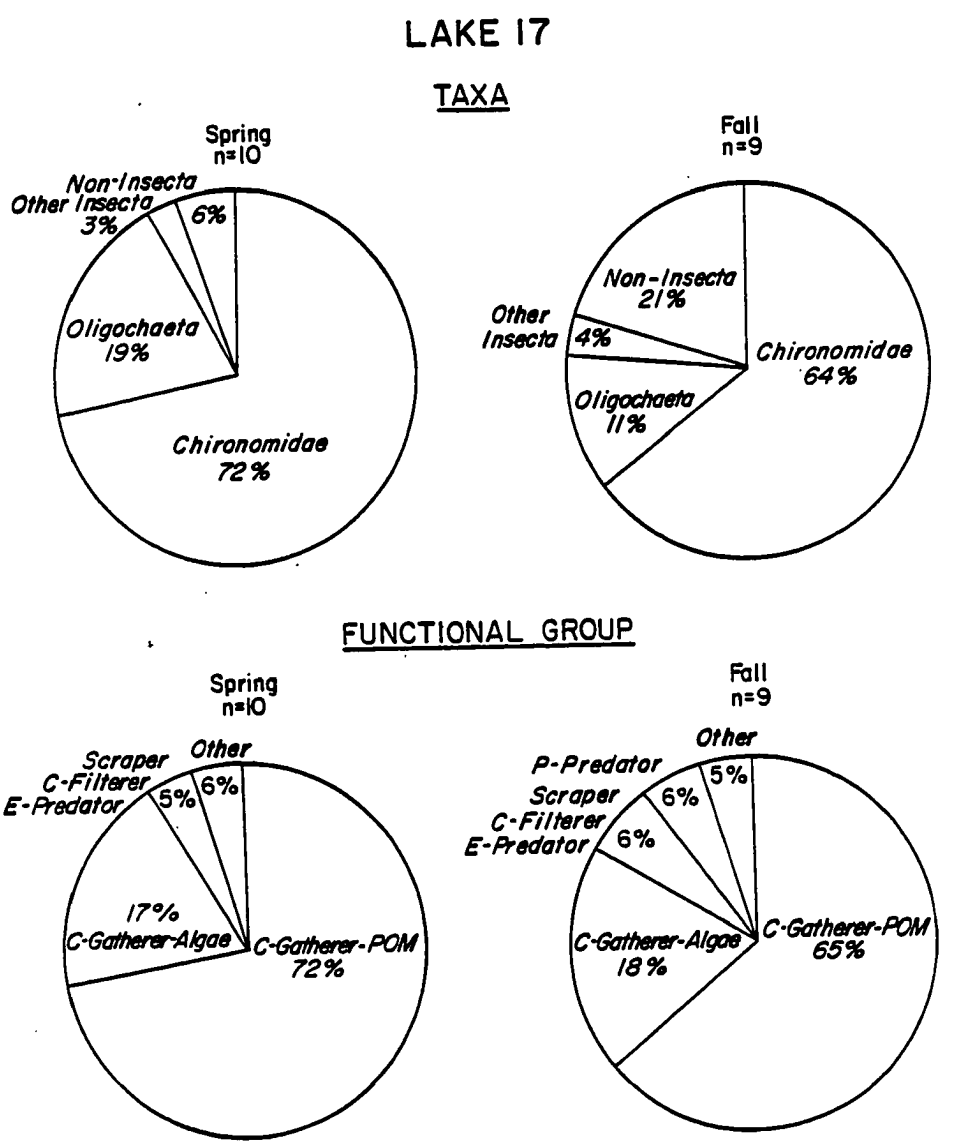

Figure 19. Summary of biovolumes of major benthic taxa and functional feeding groups in spring (19 June - 4 July) and fall (29 August - 11 September) in Lake 17, Scottie-Desper Creeks Study Area, Alaska, 1979.

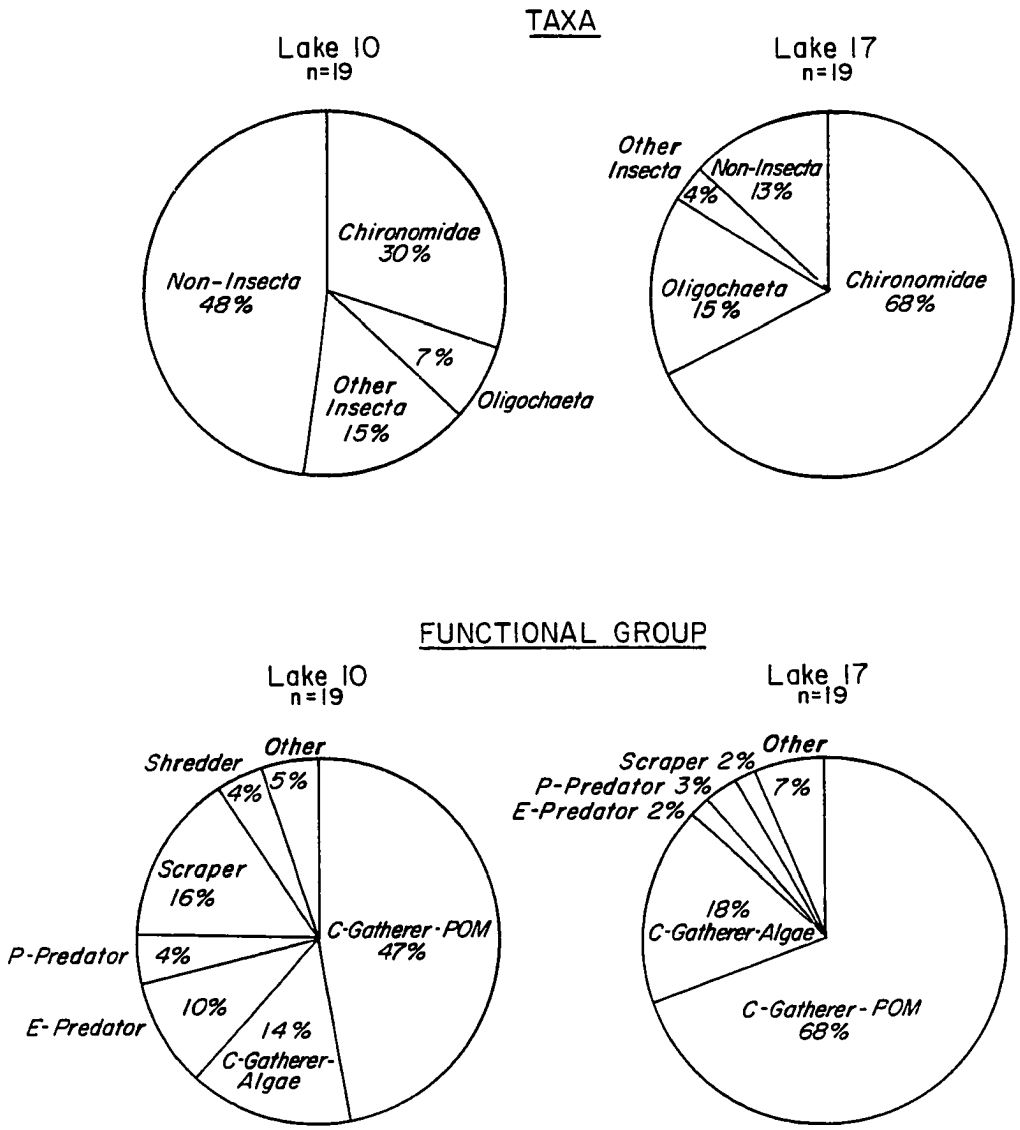

Figure 20. Summary of biovolumes of major benthic taxa and functional feeding groups in Lakes 10 and 17 (combined spring and fall data), Scottie-Desper Creeks Study Area, Alaska, 1979.

In contrast, Lake 17 was dominated by Chironomidae and Oligochaeta, comprising over 90% of total biovolume in spring and 75% in fall (Figure 19). In Lake 17, non-Insecta comprised only 6% and 21% in spring and fall, respectively, with other Insecta comprising 3% and 4% in spring and fall, respectively.

In both lakes, collector-gatherers of POM was the dominant functional feeding group at both sampling periods, comprising 39% of total fall biovolume in Lake 10 (Figure 18) and as much as 72% (spring) in Lake 17 (Figure 19). Collector-gatherer-algae was the second largest group in Lake 17, comprising 17% of total biovolume in spring and 18% in fall. This group was also important in Lake 10, particularly in fall when it comprised 22% of total biovolume.

All other functional feeding groups in Lake 17 (Figure 19) were relatively unimportant, with none exceeding 6% of total biovolume in either sampling period. In contrast, scrapers and engulfer-predators in Lake 10 (Figure 18) comprised sizeable proportions of total biovolume in spring (18% and 3%, respectively) and fall (18% and 14%, respectively).

Because major taxa and functional feeding groups were generally similar in spring and fall within a given lake (Figure 20), combined samples for each lake show essentially the same patterns. Non-Insecta were dominant in Lake 10 and Chironomidae in Lake 17. Collector gatherer-POM was the dominant functional feeding group in both lakes, with scrapers and engulfer-predators comprising noticeably larger proportions in Lake 10 than in Lake 17.

DIFFERENCES IN MACROINVERTEBRATE COMMUNITIES

Tables 7-15 are summaries of significant differences in proportions of numbers and/or biovolumes of taxa and functional groups between 1) spring and fall (Tables 7 and 8); 2) deep and shallow strata within each lake (Tables 9-12); and 3) Lakes 10 and 17 (Tables 13-15). In general, analyses of numerical data (Tables 7, 9, 11) resulted in significant differences between more groups than corresponding analyses of volumetric data (Tables 8, 10, 12). Also, most groups significantly different in proportions of biovolumes were also different in proportions of numbers.

BETWEEN SEASONS

In Figure 18, the composition of major taxa in Lake 10 was relatively similar between spring and fall. Higher proportions of biovolumes of non-Insecta in Lake 10 in spring (Figure 18) were probably due to significantly greater biovolumes of Conchostraca and Amphipoda (Table 8). Similarly, the greater biovolumes of Insecta in Lake 10 in fall were probably due to greater biovolumes of Lestidae (Odonata) (although biovolumes of Chaoboridae were also greater in fall).

In Lake 17, biovolumes of several groups were significantly different (Table 8); four genera of Chironomidae (Tanypus, Cricotopus, Dicrotendipes, Cryptochironomus), three non-insect taxa (Turbellaria, Hirudinea and Hyalella) and two functional feeding groups (piercer-

Table 7. Summary of significant differences in proportions of numbers (Mann-Whitney - U test) of benthic macroinvertebrates between samples collected in spring (19 June - 4 July) and fall (29 August - 11 September) of Lakes 10 and 17, Scottie-Desper Creeks Study Area, Alaska, 1979.

Variable type	Greater in Lake No.	Significance level P<0.01	Significance level P<0.05
	********** LAKE 10 **********		
Taxon	Spring	Conchostraca	--
	Fall	--	Other Insecta
	Fall	--	Gyrinidae
Functional group	Fall	Engulfer-predator	--
	********** LAKE 17 **********		
Taxon	Spring	Turbellaria	--
	Spring	--	Cricotopus
	Fall	Dicrotendipes	--
	Fall	Cryptochironomus	--
	Fall	--	Hyalella
	Fall	--	Hirudinea

Table 8. Summary of significant differences in proportions of biovolumes (Mann-Whitney - U test) of benthic macroinvertebrates between samples collected in spring (19 June - 4 July) and fall (29 August - 11 September) of Lakes 10 and 17, Scottie-Desper Creeks Study Area, Alaska, 1979.

Variable type	Greater in:	Significance level P<0.01	P<0.05
	********** LAKE 10 **********		
Taxon	Spring	Conchostraca	--
	Spring	--	Amphipoda
	Spring	--	Lestidae
	Fall	Chaoboridae	--
Functional group	Fall	--	Engulfer-predator
	********** LAKE 17 **********		
Taxon	Spring	Turbellaria	--
	Spring	--	Tanypus
	Spring	--	Cricotopus
	Fall	Dicrotendipes	--
	Fall	Cryptochironomus	--
	Fall	--	Hirudinea
	Fall	--	Hyalella
Functional group	Fall	--	Piercer-predator
	Fall	--	Total predator

Table 9. Summary of significant differences in proportions of numbers (Mann-Whitney - U test) of benthic macroinvertebrates between samples collected in shallow (≤ 1.0 m) and deep (> 1.0 m) strata in spring and fall of Lake 10, Scottie-Desper Creeks Study Area, Alaska, 1979.

Variable type	Greater in:	Significance level P<0.01	Significance level P<0.05
	********** SPRING ********** (19 June - 4 July)		
Taxon	Shallow	--	Other Insecta
	Shallow	Lestidae	--
	Shallow	--	Hirudinea
	Shallow	Planorbidae	--
	Shallow	--	Hyalella
	Shallow	--	Amphipoda
	Shallow	--	Dytiscidae
	Shallow	--	Ceratopogonidae
	Shallow	--	Corixidae
	Shallow	--	Other Chironomidae
Functional group	Shallow	--	Collector-gatherer algae
	Shallow	--	Piercer-predator
	Shallow	--	Total predator
Environmental	Deep	--	Wood
	********** FALL ********** (29 August - 11 September)		
Taxon	Shallow	Conchostraca	--
	Shallow	--	Hirudinea
	Shallow	--	Sphaeriidae
	Shallow	--	Coenagroinidae
	Shallow	--	Odonata
	Shallow	--	Other Chironomidae
Functional group	Shallow	--	Collector-filterer
	Deep	--	Engulfer-predator
	Shallow	--	Total collector - gatherer
Environmental	Shallow	--	Vegetation

Table 10. Summary of significant differences in proportions of biovolumes (Mann-Whitney - U test) of benthic macroinvertebrates between samples collected in shallow (≤ 1.0 m) and deep (> 1.0 m) strata in spring and fall of Lake 10, Scottie-Desper Creeks Study Area, Alaska, 1979.

Variable type	Greater in:	Significance level P<0.01	Significance level P<0.05
	********** SPRING ********** (19 June - 4 July)		
Taxon	Shallow	--	Other Insecta
	Shallow	Lestidae	--
	Shallow	--	Planorbidae
Functional group	Shallow	--	Engulfer-predator
Environmental	Deep	--	Wood
	********** FALL ********** (29 August - 11 September)		
Taxon	Shallow	Conchostraca	--
	Shallow	--	Coenagroinidae
	Shallow	--	Odonata
	Shallow	--	Phryganeidae
	Shallow	--	Other Chironomidae
Functional group	Shallow	--	Shredder
Environmental	Shallow	--	Vegetation

Table 11. Summary of significant differences in proportions of numbers (Mann-Whitney - U test) of benthic macroinvertebrates between samples collected in shallow (≤ 1.0 m) and deep (> 1.0 m) strata in spring and fall of Lake 17, Scottie-Desper Creeks Study Area, Alaska, 1979.

Variable type	Greater in:	Significance level P<0.01	Significance level P<0.05
	********** SPRING ********** (19 June - 4 July)		
Taxon	Shallow	Corixidae	--
	Shallow	Glyptotendipes	--
	Shallow	Cricotopus	--
	Shallow	--	Turbellaria
	Shallow	--	Ostracoda
	Deep	--	Chaoboridae
Functional group	Deep	--	Engulfer-predator
Environmental	Shallow	Wood	--
	Shallow	--	Vegetation
	********** FALL ********** (29 August - 11 September)		
Taxon	Shallow	--	Hirudinea
	Shallow	--	Dicrotendipes
	Shallow	--	Other Chironomidae
	Deep	--	Nematoda
	Deep	--	Sphaeriidae
	Deep	--	Chironomus
Functional group	Shallow	--	Piercer-predator
	Deep	--	Engulfer-predator
	Deep	--	Collector-filterer
Environmental	Shallow	--	Wood

Table 12. Summary of significant differences in proportions of biovolumes (Mann-Whitney - U test) of benthic macroinvertebrates between samples collected in shallow (≤ 1.0 m) and deep (> 1.0 m) strata in spring and fall of Lake 17, Scottie-Desper Creeks Study Area, Alaska, 1979.

Variable type	Greater in:	Significance level P<0.01	Significance level P<0.05
	********** SPRING ********** (19 June - 4 July)		
Taxon	Shallow	Glyptotendipes	--
	Shallow	Cricotopus	--
	Shallow	--	Turbellaria
Environmental	Shallow	Wood	--
	Shallow	--	Vegetation
	********** FALL ********** (29 August - 11 September)		
Taxon	Shallow	--	Non-Insecta
	Shallow	--	Other Insecta
	Shallow	--	Hirudinea
	Shallow	--	Nematoda
	Shallow	--	Hyalella
	Shallow	--	Glyptotendipes
	Shallow	--	Dicrotendipes
	Shallow	--	Other Chironomidae
	Deep	--	Chironomus
	Deep	--	Chironomidae
Functional group	Shallow	--	Total predator
	Shallow	--	Total other
	Deep	--	Total collector-gatherer
Environmental	Shallow	--	Wood

Table 13. Spring summary of significant differences in proportions of biovolumes (Mann-Whitney - U test) of benthic macroinvertebrates between Lakes 10 and 17, Scottie-Desper Creeks Study Area, Alaska, 1979.

Variable type	Greater in Lake No.	Significance level P<0.01	P<0.05
Taxon	10	Non-Insecta	--
	10	Hirudinea	--
	10	Hyalella	--
	10	Conchostraca[1]	--
	10	--	Turbellaria
	10	--	Planorbidae
	10	--	Amphipoda
	10	--	Lestidae[1]
	10	--	Coegnagrionidae[1]
	10	--	Dytiscidae[1]
	17	--	Nematoda
	17	--	Chironomidae
Functional group	10	Piercer-predator	--
	10	--	Scraper
	10	--	Total predator
	10	--	Total other
	10	--	Shredder[1]
Environmental	10	Vegetation	--

[1] Groups absent in Lake 17.

Table 14. Fall summary of significant differences in proportions of biovolumes (Mann-Whitney - U test) of benthic macroinvertebrates between Lakes 10 and 17, Scottie-Desper Creeks Study Area, Alaska, 1979.

Variable type	Greater in Lake No.	Significance level P<0.01	P<0.05
Taxon	10	Other Insecta	--
	10	Valvatidae	--
	10	--	Chaoboridae[1]
	10	--	Conchostraca[1]
	10	--	Coenagrionidae[1]
	10	--	Odonata[1]
	17	--	Chironomidae
	17	--	Oligochaeta
	17	--	Nematoda
Functional group	10	--	Scraper
	10	--	Engulfer-predator
	10	--	Total predator
	17		Total collector-gatherer
Environmental	10	Vegetation	--

[1]Groups absent in Lake 17.

Table 15. Combined (spring/fall) summary of differences in proportions of biovolumes (Mann-Whitney - U test) of benthic macroinvertebrates between Lakes 10 and 17, Scottie-Desper Creeks Study Area, Alaska, 1979.

Variable type	Greater in Lake No.	Significance level P<0.01	P<0.05
Taxon	10	Other Insecta	--
	10	Non-Insecta	--
	10	Hirudinea	--
	10	Valvatidae	--
	10	Conchostraca[1]	--
	10	Lestidae[1]	--
	10	Dytiscidae[1]	--
	10	Coenagrionidae[1]	--
	10	Odonata[1]	--
	17	Chironomidae	--
	17	--	Oligochaeta
	17	--	Nematoda
Functional group	10	Engulfer-predator	--
	10	Scraper[1]	--
	10	Shredder[1]	--
	10	Total predator	--
	10	Total other	--
	10	--	Piercer-predator
	17	Total collector-gatherer	--
Environmental	10	Vegetation	--

[1]Groups absent in Lake 17.

predator and total predator). Although biovolumes of several individual taxa were significantly different between spring and fall, major taxonomic groupings were relatively stable (Figure 19). The noticeably higher biovolumes of non-Insecta in fall (not significantly higher) were due to higher biovolumes of Hirudinea, Hyalella and Nematoda in the shallow stratum (Table 12).

BETWEEN DEPTHS

The most obvious trend evident in Tables 9 - 12 is that numbers and biovolumes of the majority of taxa and functional groups were greatest in the shallow stratum. Factors such as increased habitat heterogenity (due to greater amounts of vegetation), and more favorable dissolved oxygen and light conditions undoubtedly constitute more favorable habitat for many taxa. Exceptions to this pattern occurred in Table 9 (engulfer-predator), Table 11 (spring; engulfer-predator: fall; Nematoda, Sphaeriidae, Chironomus, engulfer-predator and collector-filterer), and Table 12 (Chironomus, Chironomidae and total collector-gatherer).

BETWEEN LAKES

Tables 13-15 are summaries of significant differences in biovolumes of taxa and functional groups between Lakes 10 and 17. Several taxa (Conchostraca, Odonata, Lestidae, Coenagroinidae, Dytiscidae) and one functional group (shredder) were totally absent

from Lake 17. In spring (Table 13), only Nematoda and Chironomidae in Lake 17 had significantly greater biovolumes than Lake 10, whereas in fall (Table 14), Nematoda, Chironomidae, Oligochaeta and total collector-gatherer were significantly greater in Lake 17. Note that all predator groups (piercer, engulfer and total predator) are significantly greater in Lake 10. This is undoubtedly related to the absence of fish predators in Lake 10. Similarly, the greater amounts of vegetation in Lake 10 (Tables 13-15) may account for the significantly greater biovolumes of shredders in Lake 10.

COMMUNITY STRUCTURE ALONG ENVIRONMENTAL GRADIENTS

Principal component analyses were performed on numerical and volumetric data for both sampling periods in each lake. However, because the primary objective was to identify associations of cohabitating taxa along several environmental gradients, use of volumetric data is less appropriate than numerical data. Therefore, numerical data are presented here (Figures 21-24), and results from analyses on volumetric data are provided in Appendix Figures C-1 to C-4 for comparison.

LAKE 10

Figures 21 and 22 are ordinations of environmental and taxonomic variables in Lake 10 for spring and fall sampling periods, respectively. The percent of total variation accounted for on the first two components for spring and fall data were 51% and 57%,

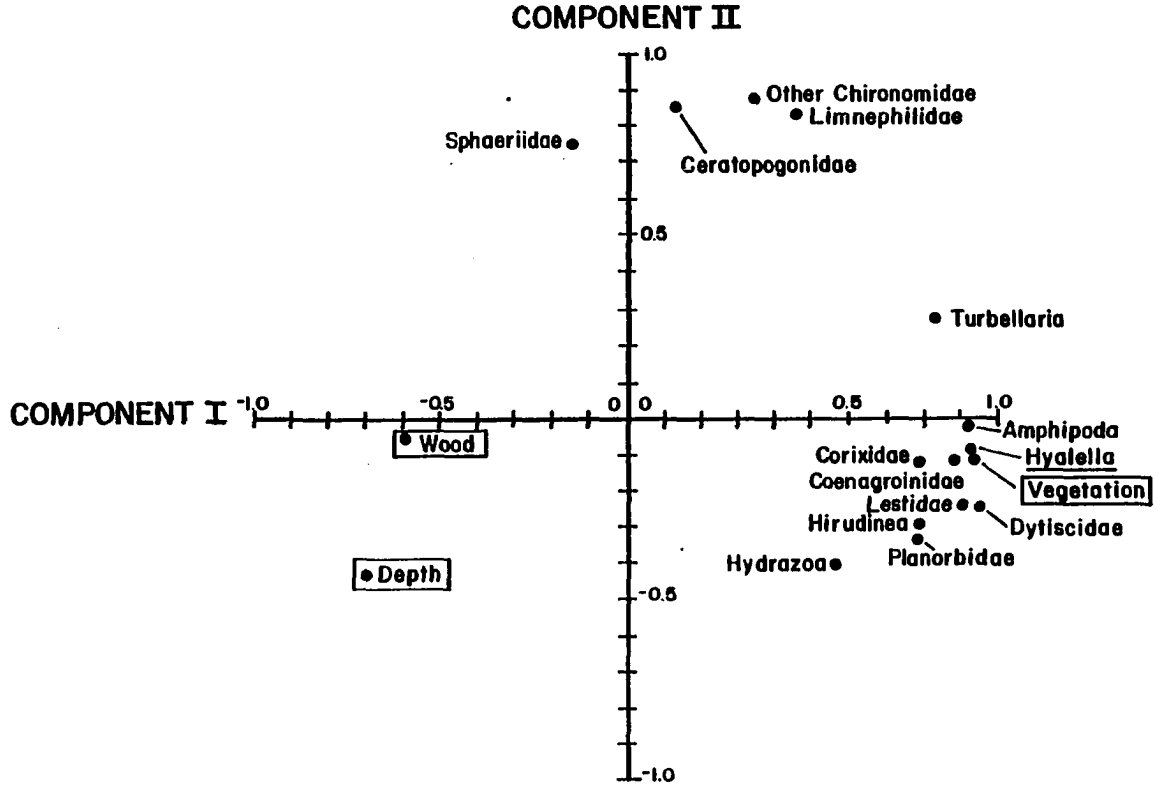

Figure 21. Ordination of environmental and taxonomic variables for spring/numerical data for Lake 10, Scottie-Desper Creeks Study Area, Alaska, 1979. Fifty-one percent of total variation was accounted for on Components I and II (34% and 17%, respectively).

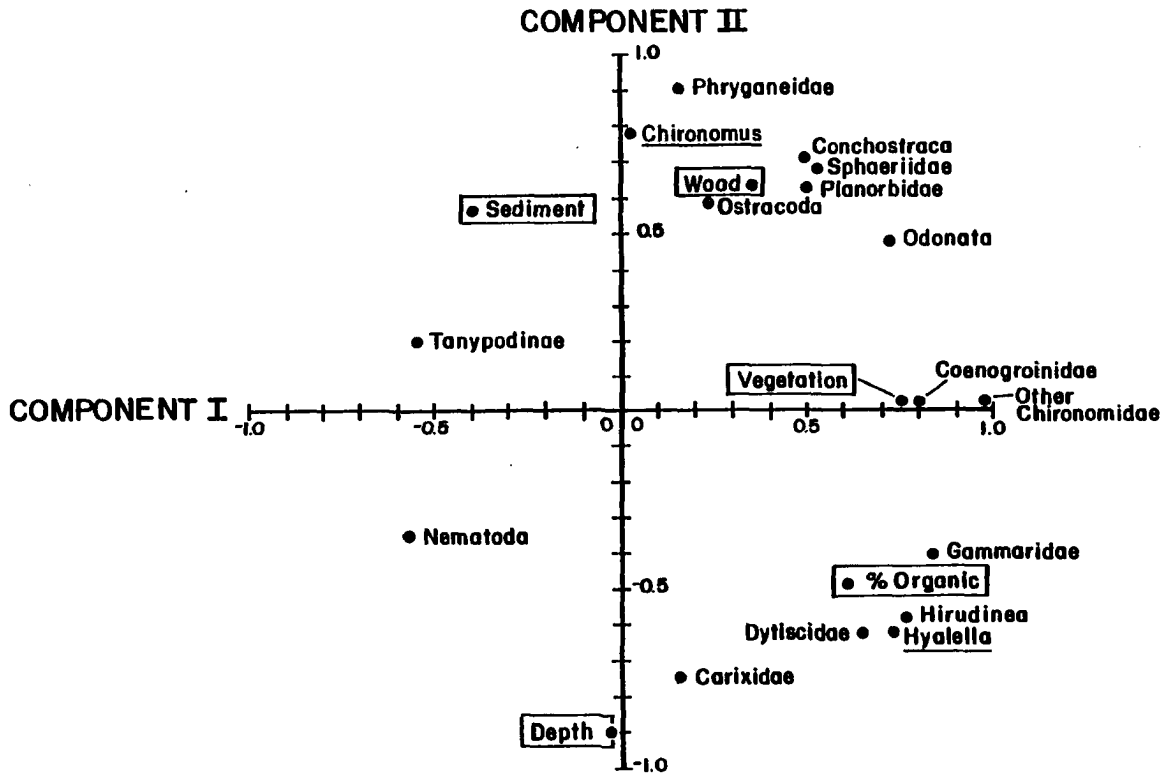

Figure 22. Ordination of environmental and taxonomic variables for fall/numerical data for Lake 10, Scottie-Desper Creeks Study Area, Alaska, 1979. Fifty-seven percent of total variation was accounted for on Components I and II (34% and 23%, respectively).

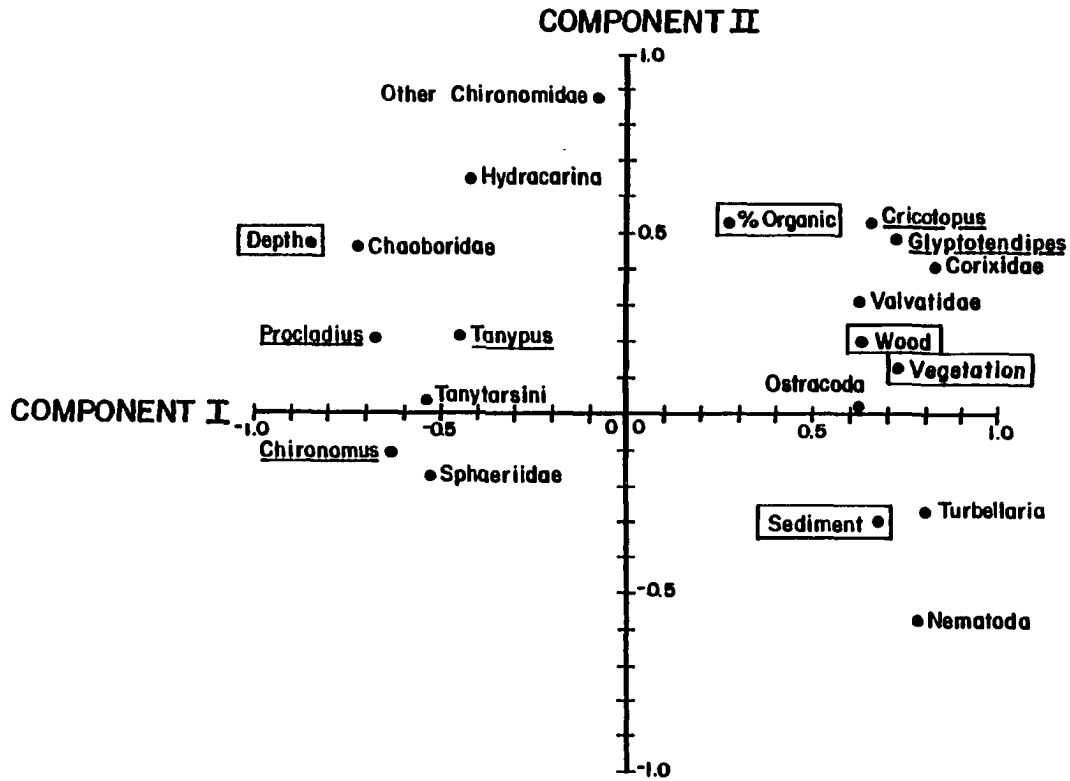

Figure 23. Ordination of environmental and taxonomic variables for spring/numerical data for Lake 17, Scottie-Desper Creeks Study Area, Alaska, 1979. Fifty-three percent of total variation was accounted for on Components I and II (37% and 16%, respectively).

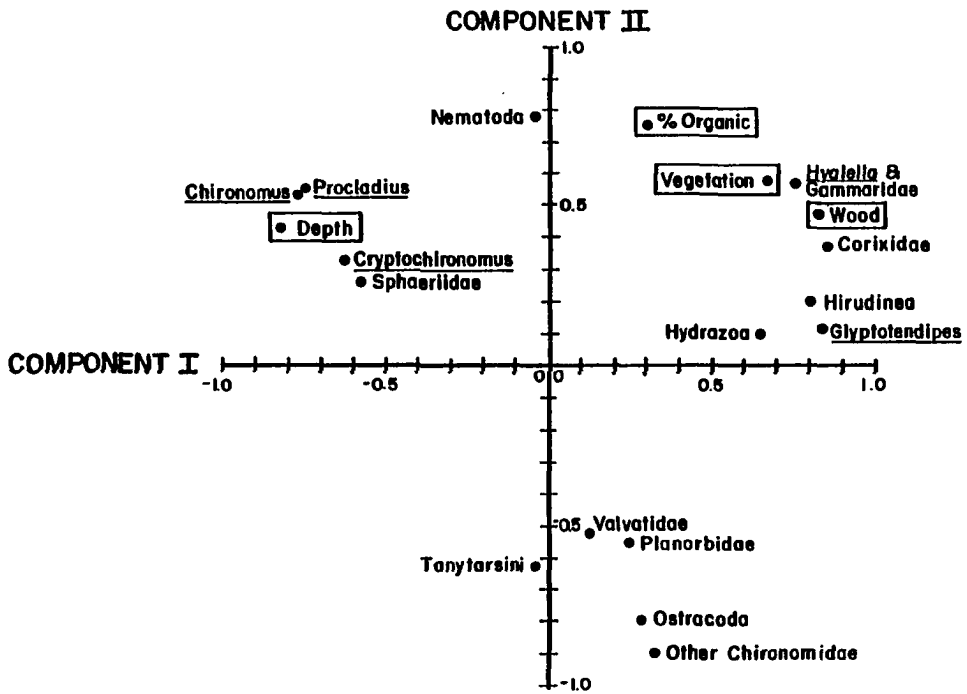

Figure 24. Ordination of environmental and taxonomic variables for fall/numerical data for Lake 17, Scottie-Desper Creeks Study Area, Alaska, 1979. Fifty-five percent of total variation was accounted for on Components I and II (31% and 24%, respectively).

respectively, with 34% accounted for on the first axis in both seasons. In Lake 10 two distinct associations of organisms were identified in spring (Figure 21). The first component was comprised of taxa that are generally large and mobile, positively correlated with vegetation and negatively correlated with depth and wood.

With the exception of Limnephilidae, Component II was comprised of taxa that were less mobile and typically found within sediments or upon the sediment surface. Collectively they occupied relatively deeper, less vegetated areas than the association of organisms that loaded on Component 1.

In fall (Figure 22) the association of taxa and environmental variables is less well defined, and the composition of recognizable associations differs from those of spring. In spring (Figure 21), depth and vegetation were contrasted on Component I, wereas in fall (Figure 22) depth and vegetation loaded on different components. In Figure 19, most separation between groups of organisms occured along Component II. An association of taxa characterized by a high degree mobility is positively associated with deeper water and more vegetation (lower right quadrant). This association is basically a subset of the association of spring taxa identified with shallow/vegetated conditions. At the positive end of Component II there is a more diverse association of organisms comprised of members that generally are more limited in mobility (Chironomus, Sphaeriidae, Ostracoda, Conchostraca and Planorbidae) as well as two taxa that are very mobile (Phryganeidae and Odonata). This diverse association is widely separated from the highly mobile association on Component II and with

the exception of Odonata, are non-overlapping on Component I. It is most similar to the sediment-related association identified in spring (Figure 18).

LAKE 17

The ordination pattern (Figure 23) in spring for Lake 17 is most clearly separated along Component I into two rather discrete groups. Shallow water, high organic content, high wood, vegetation, and sediment is associated with higher proportions of Cricotopus, Glyptotendipes, Corixidae, Valvatidae, Ostracoda, Turbellaria and Nematoda. This group is contrasted to the association of taxa positively correlated with depth including various chironomid groups (Chironomus, Procladius, Tanytarsini, Tanypus, and other Chironomidae) as well as Hydracarina, Chaboridae and Sphaeriidae.

A similar association of taxa, positively related to depth, is also present in fall (Figure 24; upper left quadrant). It is one of three associations identifiable in fall. Component I essentially separates variables into three groups, shallow, mid and deep water associations that are characteristicly different. Taxa loading positively on Components I and II are large and mobile (Hyalella, Gammaridae, Corixidae and Hirudinea). This association of taxa typified a shallow vegetated area with sediments of high organic content.

Both remaining groups of organisms were primarily composed of various taxa of Chironomidae and/or Gastropoda. Both groups were more

similar to each other than to the shallow-water group containing large mobile taxa. The "deep-water" group was an association of large, relatively sedentary organisms (Chironomus, Procladius, Cryptochironomus, Nematoda[2] and Sphaeriidae). As such, they differed from the relatively large mobile taxa, characteristic of shallow, vegetated areas. The mid-depth association differed from the shallow-water group in both type and size (Valvatidae, Planorbidae, Tanytarsini, other Chironomidae and Ostracoda). They were similar in type to the deep-water group, but were generally smaller in size (other Chironomidae were a composite group of Chironomidae less than 5 mm in length).

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[2] The majority of Nematoda were large, free-living forms.

DISCUSSION

GENERAL

In any system, some components will undoubtedly have more influence on the overall organization of the system than others. Some examples of key components for aquatic systems are suggested by Brinkhurst (1974) as those organisms that add physical structure to the habitat (e.g. macrophytes), those that modify habitat via digging or burrowing (e.g. carp or tube-dwelling polychaetes), those that physically force out other species (e.g. intertidal mussels), or carnivores (e.g. fish) that constitute a selective pressure on prey species.

Lakes 10 and 17 were both relatively small thaw lakes located approximately 1 km apart, situated along the edge of a glacial outwash fan which protrudes northward from the foothills of the Alaska Range. Both are subjected to similar climatic conditions and were formed by the same ice thaw processes (Wallace 1948). Both were hydrologically connected to the Scottie-Desper Creek system by surface channels and both contained fine-grained mud bottoms. Lake 10 was smaller, shallower and less uniform in shape than Lake 17. Lake 10 contained abundant macrophytes and no fish, whereas, Lake 17 contained virtually no macrophytes but an apparently dense population of humpback whitefish.

Because the two lakes were similar to each other in such fundamental ways as climate, lake origin and hydrological association with a nearby creek system, their respective communities of benthic

macroinvertebrates were expected to be similar. Conversely, because these two lakes differed substantially with respect to relative amounts of rooted macrophytes and fish predators, as well as lake size and depth, their respective benthic faunas were also expected to reflect these habitat differences (Zaret 1980).

The basic organization of macroinvertebrates in Lakes 10 and 17 was similar in several fundamental ways. Both lakes contained a unimodal distribution of total biovolume with depth (Figures 16 and 17). In both lakes, Chironomidae comprised a large proportion of total biovolume (Figure 20) and both lakes were dominated by the functional feeding group collector-gatherers, particularly collector-gatherers of POM (Figure 20). And finally, although the taxanomic composition differed between lakes in many ways, both lakes contained at least two identifiable associations of taxa that were distributed along a depth/vegetation gradient (Figures 21-24).

The general shape of the vertical distribution curve of total benthic biovolume (Figures 16 and 17) is a characteristic feature of many lakes (Brinkhurst 1974). However, the depth at which peak biovolumes (or weights) occurred, seems to be related to environmental gradients such as temperature or dissolved oxygen profiles (e.g. Jonasson 1978). In Lake 10, the peak was not well defined but seemed to occur at a depth less than 1.0 m, whereas in Lake 17, the peak biovolume occurred at a depth somewhere between 5 and 6 m. The mechanisms that maintain this characteristic feature of lakes have not been clearly identified but appear to be related to the distribution of organic matter which is in turn mediated by sediment-

transport mechanisms such as wind action interacting with the thermocline and wave action (Jonasson 1978). This similarity between Lakes 10 and 17 was not unique to these lakes but is a general characteristic of lakes.

The family Chironomidae was a dominant taxon in both lakes. It comprised 30% and 68% of the total biovolume of benthic macroinvertebrates in Lakes 10 and 17, respectively (Figure 20). This relatively large proportion of chiromomid biovolume in both lakes is not particularly striking because this taxon is widespread and common to most lake systems (e.g. Brinkhurst 1974). The benthic fauna in Lake 17 was more typical of that reported for arctic lakes (Hobbie 1980) than was the fauna of Lake 10.

The numerical dominance of Chironomidae is a characteristic of the insect faunas in arctic lakes (Oliver 1968). They generally comprise one-fifth to one-half of the total number of species in the insect fauna and in extreme cases may comprise 75 to 95% of the total biomass (Bierle 1972). Chironomidae comprised 68% of total biovolume in Lake 17 and in this respect, is similar to arctic lakes. Although the reasons for the dominance of Chironomidae in northern regions have not been clearly elucidated, it is likely that the ability to tolerate hypoxic conditions resulting from the long ice-over period (Welch 1980) and the ability to tolerate freezing (Danks 1978) would contribute to their success.

The similarity in the organization of functional feeding groups between Lakes 10 and 17 was greater (Figure 20) than that shown for

taxa. The domination of the benthos by collector-gatherers suggests that the energetic pathways in both lakes were regulated by the detrital pool. This is consistent with the view presented by Jonasson (1978) for Lake Esrom. Jonasson found that major differences occurred in the organization of the macroinvertebrate community (as herbivores, detritivores and carnivores) as habitat and food availability changed with water depth. He suggested that food was the major organizational feature accounting for the benthic community structure in the lake.

It seems likely that the dependence upon the detrital food base would become greater for lakes at higher latitudes due to the increasing length of the ice-covered period. The ice-covered period for Lakes 10 and 17 was approximately 9.5 months. Thus, it is not surprising that although these lakes differed substantially regarding the presence/absence of macrophyte and fish predators, the major food-gathering strategy (collector-gatherer) is similar in both lakes.

ASSOCIATIONS OF MACROINVERTEBRATES

In both spring and fall samples in both lakes, depth and vegetation were associated with the first principal axis (Figures 21-24) and appeared to be the primary environmental gradients along which the associations of benthic macroinvertebrates were organized. However, in fall (Figures 22 and 24) the associations were more diffuse in Lake 10, and in Lake 17 were partitioned into three rather than two distinct associations. In Lake 17, taxa included in two of the three associations were very similar to the corresponding spring associations,

with the third association comprised of an intermediate subset of taxa derived from both associations present in spring.

The associations identified in both lakes roughly corresponded to two (sometimes three) associations of benthic macroinvertebrates which have been shown to characterize the littoral and profundal regions of lakes (Wetzel 1975) over a wide range of latitudes (e.g. Johnson and Brinkhurst 1971; Jonasson 1975; Darlington 1977). However, taxonomic composition of these associations is thought to vary with trophic state (Wetzel 1975; Welch 1980) with structural complexity (e.g. Cooper and Crowder 1979) and with different levels of fish predation (e.g. Keast 1979; Ringler 1979; Zaret 1980). Since both lakes had similar nutrient levels and roughly comparable levels of benthic biovolumes (Figures 16 and 17), effects of differential trophic levels have not been considered. Instead, the organization of taxa and functional feeding groups have been evaluated in light of environmental gradients and the presence/absence of macrophytes and fish predators.

Compared to Lake 17, Lake 10 had a much greater amount of structural complexity in its littoral habitat as a result of relatively large amounts of aquatic macrophytes and relatively greater inputs of course allochthous material (e.g. leaves, bark, tree branches, etc.).

In Lake 10, a relatively tight cluster of taxa is associated with shallow water and higher amounts of vegetation (Figure 21), particularly in spring. The taxa of this association are characteristically large and mobile. Predaceous taxa such as Coenagroinidae and Lestidae and probably Dytiscidae, undoubtedly rely on vegetation to provide a structural setting within which to hunt for prey. Hydra use

macrophytes for attachment and Amphipoda and Planorbidae use it as a substrate upon which to forage for epiphytic algae and associated microorganisms.

The other association present in spring contained fewer taxa. It was not distinctly separated on the first principal axis but was separated on the second principal axis. With the exception of Limnephilidae, distributional patterns of these taxa are more related to sediments than vegetation.

In fall, the associations were much more diffuse and were organized differently than in spring. Vegetation was not a major organizational feature. Large mobile taxa were associated with the deeper water (Corixidae, Dytiscidae, Hirudinea, Gammaridae and Hyalella) and more sediment-related taxa were present in the shallow water (e.g. Chironomus, Ostracoda, Planorbidae, Sphaeriidae, Conchostraca). Although the reasons for the differences between associations in spring and fall are unknown, it may be due to a shift in importance of other environmental factors such as temperature and dissolved oxygen. In fall, major taxa present in the near-shore area are known to be tolerant of conditions of freezing and hypoxia (Danks 1978) (e.g. Chironomidae, Planorbidae) or else are taxa likely to overwinter as eggs (e.g. Ostracoda, Conchostraca). Alternatively, the large mobile taxa occupying the off-shore areas are likely to overwinter as adults. Relatively low and variable dissolved oxygen conditions in fall (refer to Figure 6: Limnology) may in part account for movement of mobile taxa to deeper water.

The associations of benthic invertebrates in Lake 17 were relatively similar between spring and fall and were more distinct from each

other than were associations in Lake 10. At both lakes, depth was contrasted to vegetation, wood and percent organic matter on the first principal component. In both spring and fall associations, there were relatively more chironomid taxa associated with deeper water (off-shore association) and relatively more non-chironomid groups associated with shallower water, more wood, vegetation and higher organic content (near-shore association). For example, in spring, the off-shore association was composed of five groups of chironomids (Chironomus, Procladius, Tanypus, Tanytarsini and other Chironomidae) and three non-chironomid groups (Chaoboridae, Sphaeriidae and Hydracarina), whereas the near-shore association contained only two chironomid groups (Glyptotendipes and Cricotopus) and five non-chironomid groups (Corixidae, Valvatidae, Ostracoda, Turbellaria and Nematoda). This same trend also occurred in fall (Figure 24). Associations in deep, mid and shallow water contained decreasing numbers of chironomid groups (three, two, and one, respectively) and increasing numbers of non-chironomid groups (one, three and five, respectively).

The near-shore associations in both spring and fall (Figures 23 and 24) contained taxa that were characterized by a diversity of life styles, undoubtedly reflecting the greater habitat diversity and more favorable dissolved oxygen conditions (refer to Figure 8: Limnology Study). Also, this habitat affords more refuges from fish predation for corixids and valvatid snails in spring (Figure 23) as well as amphipods, corixids and leeches in fall (Figure 24).

The offshore associations were similar between spring and fall. This habitat contained less structural material than the near-shore area and was undoubtedly strongly influenced by physical stresses

such as lower levels of dissolved oxygen and colder temperatures (refer to Figure 8: Limnology).

ROLE OF FISH PREDATION

There are several lines of evidence that suggest that fish predation in Lake 17 exerted a strong selective impact on the benthic macroinvertebrate community structure. This lake contained an apparently dense population of humpback whitefish (Coregonus pidschian) that exhibited a remarkable flexibility in diet. Guts of fish captured during mid-day contained primarily chironomids whereas guts of fish captured in early evening and in off-shore areas contained primarily cladocerans (refer to Figure 13: Fish Study). For the purposes of this discussion humpback whitefish in Lake 17 were assumed to be generalist feeders, likely to consume all prey in proportion to their availability. Because most fish were adults, it was assumed that they were not gape-limited (i.e. able to consume all sizes of macroinvertebrates available [Zaret 1980]).

The direct selective effects of large size have been clearly demonstrated for zooplankton (Brooks and Dodson 1965; Werner and Hall 1974) and seem to apply to macrobenthos as well (e.g. Macan 1977a,b, Zaret 1980). In several studies where either fish were removed or added to natural systems, results have shown that fish tend to selectively consume large macrobenthic invertebrates (Ball and Hayne 1952; Kajak 1977; Macan 1977b; Stenson 1979). In addition, it has been proposed that predation by fish may restrict the breadth of the

predator niche (Kajak 1977) but this remains to be clearly demonstrated.

Although differences in sizes of benthic invertebrates between Lakes 10 and 17 were not quantitatively analyzed, there were some obvious differences in both size and function of some taxa. Lake 10 contained several large, conspicuous taxa that were totally absent or had significantly lower proportions of biovolumes in Lake 17. These taxa included two families of odonates, dytiscid beetles, leeches and conchostracans (Table 15). In addition to their large size, these taxa are generally active and mobile and therefore are relatively conspicuous, easily detected in the littoral zones of lakes by casual observation. The fact that these taxa were absent from the guts of fish in Lake 17 (Fish Study) does not necessarily indicate that they are not actively excluded by fish because the prey present in fish guts at any point in time are likely to be ones which remain after fish have previously eliminated their most selected prey. Thus, contents of fish guts may only reflect prey selection from an array of ecological leftovers (Drenner and McComas 1980).

Lake 17 lacked an abundance of large, conspicuous benthic taxa. Sixty-eight percent of the total biovolume was comprised of chironomids, of which Chironomus and Glyptotendipes were the dominant genera. In addition to the lack of large and conspicuous taxa, Lake 17 also differed with respect to functional feeding groups (Table 15). In Lake 17, predators (piercer and engulfer) had significantly lower biovolumes. For combined spring/fall samples the list of predatory taxa include Hirudinea, Lestidae, Coenagroinidae, Dytiscidae, with

Turbellaria in spring only (Table 13) and Chaoboridae in fall only (Table 14). It is possible that the absence of these taxa in Lake 17 was due to factors other than fish predation. However, it is more likely that their absence was at least in part, a result of size selective fish predation as well as interspecific competition for a common food resource. Thus, large invertebrate predators such as those listed above would be at a disadvantage because of size, as well as having a smaller forage base as a result of fish predation.

ROLE OF MACROPHYTES

The presence of whitefish in Lake 17 seems to be a reasonable explanation for the lack of abundance (or biovolume) of large predaceous macroinvertebrates in the shallow region of this lake. However, the simple presence or absence of macrophytes may also account for differences in occurrence of some taxa, irrespective of the effects of fish predation.

Biovolumes of both shredders and grazers were significantly greater in Lake 10 where macrophytes were abundant (Table 13). For shredders (Trichoptera) this may be due to the availability of an adequate supply of material upon which to forage. For scrapers, it is probably due to an increase in the quantity of substrate area from which to scrape epiphyton.

SUMMARY/CONCLUSIONS

LIMNOLOGY

The Scottie-Desper Creeks Study Area is located in the upper Tanana River Valley (N62° 38'; W141° 10'). The area is underlain with permafrost (Selkregg 1976) and fine grained sediments (Wallace 1948) and consists of a mosaic of meandering creeks and numerous, small lakes formed by the sinking of unfrozen pockets of the permafrost basin (Wallace 1948). Over time, small isolated lakes enlarge via continued melting of the permafrost. This melting fuses the small lakes into a complicated series of larger connected lakes which eventually become isolated again via a system of levees that form along the water courses. This process of lake formation and development has resulted in a continuum of lake types differing in size and degree of hydrological association (isolated or connected) with Scottie Creek.

Although it was not possible to fully determine the nature and degree to which Scottie Creek influences lake hydrology it was apparent that the condition of hydrological isolation or connection to Scottie Creek strongly effected physical and chemical characteristics of lakes in the area. Isolated lakes were more homogenous as a group (based on physical and chemical characteristics) and were generally warmer and had lower pH, alkalinity, hardness and dissolved phosphorus than connected lakes (Figures 6 and 7).

The degree of hydrological interchange of a lake with Scottie Creek would undoubtedly effect flux rates of dissolved and particulate

carbon and nutrients. This may account for the relatively higher nutrient levels measured in connected lakes as well as the greater heterogeneity evident within this group.

Two connected type lakes (Lake 10 and 17) were selected for more intensive study. Both lakes had relatively high levels of dissolved nutrients, approximating those of Ace-Deuce Lakes (Table 2), which are relatively productive compared to other interior Alaska lakes (Alexander and Barsdate 1974). However, Lake 10 was only connected to Scottie Creek during high water events when water levels were able to breach a small beaver dam at its outlet. It was smaller, and shallower than Lake 17 and contained a well developed littoral region but few fish. Conversely, Lake 17 was a relatively large, deep lake, continuously connected to Scottie Creek (during the open-water period) via surface water connections. Lake 17 contained a poorly developed littoral region and relatively dense population of humpback whitefish.

Seasonal depth profiles for temperature and dissolved oxygen suggested that lake dynamics were substantially different for Lakes 10 and 17. Lake 10 was subject to short-term, wind-induced lake turnover, whereas Lake 17 appeared to be a dimictic lake maintaining a thermocline and clinograde oxygen curve throughout the summer.

FISH STUDY

Because Lake 10 contained few fish, this study was conducted in Lake 17 only. Adult humpback whitefish (*C. pidschian*) was the only fish species present in Lake 17 in significant numbers. These fish

apparently entered Lake 17 in spring, fed heavily during the summer on Chironomidae and Cladocera and then emigrated in fall to spawn and/or overwinter elsewhere. Results of analyses of variance based upon numbers and biovolumes of prey items in fish stomachs showed significant differences in diet between fish captured in different water depths, and at different times of day and year.

Fish in shallow water ($\leq$ 1.0 m) fed primarily on chironomids, whereas fish in deeper water (> 1.0 m) fed almost exclusively on Cladocera (not verified in fall). Although biovolumes of chironomids never comprised less than 35% at any time of day sampled, composition of the diet changed significantly at different times of day. Chironomids were used most heavily around noon (75% Chironomidae; 5% Cladocera) and Cladocera was used most heavily in early morning (Chironomidae 35%; Cladocera 42%) and late afternoon (Chironomidae 39%; Cladocera 46%) with concomitant decreases in the proportion of chironomid biovolume. Differences in diet between fish captured at different times of year (spring, fall) were expected due to growth and emergence of various prey taxa over time, and were therefore largely ignored.

The abrupt changes in diets of fish obtained at different depths and different times of day suggest that fish "switched" prey types, possibly due to changes in visibility of prey and/or changes in relative prey densities. Because chironomids and cladocerans occupy different habitats, successful predation on both prey types necessitates the use of at least two feeding modes (benthic particulate and palagic particulate). Because a few fish stomachs contained high

numbers of Cladocera (30,000-50,000), in excess of what could be consumed via a particulate feeding mode, a third feeding mode (pelagic gulping) was hypothesized for conditions of high cladoceran density.

BENTHIC INVERTEBRATE STUDY

The benthic macroinvertebrate communities of Lakes 10 and 17 were compared on the basis of taxa and functional feeding groups. These lakes were selected because they differed substantially in the relative contribution of littoral macrophytes as an autochthonous carbon source and in the relative importance of fish predation. It was anticipated that the presence/absence of these factors would substantially affect the community structure of aquatic macroinvertebrates.

In both lakes, Chironomidae was the dominant taxon and collector-gatherers (POM and algae) the dominant functional feeding group (by volume). In addition, two basic communities of invertebrates were identified (using principal component analyses) in both lakes (nearshore and offshore communities). In both lakes the nearshore community was characterized by organisms that were highly mobile (e.g. Amphipoda, Corixidae, Hirundinea), whereas the offshore community in both lakes was relatively sedentary (e.g. Chironomidae, Oligochaeta, Sphaeriidae).

Although the lakes exhibited some fundamental similarities, in composition of taxa and functional feeding groups, they differed substantially in several ways. Lake 10 contained significantly greater total biovolumes of invertebrates per sample as well as significantly

greater biovolumes of shredders and predators (engulfer and piercer). In addition, several predatory taxa present in Lake 10 were totally absent in Lake 17 (e.g. Lestidae, Coenagroinidae, Aeshnidae, Dytiscidae, Gyrinidae and Haliplidae). The presence of the greater abundance of these relatively large-sized predators and non-predatory (Amphipoda and Conchostraca) taxa in Lake 10 was attributed to the lack of fish predation, whereas the presence of significantly greater biovolume of shredders was attributed to the presence of greater amounts of macrophytes and allochthonous carbon inputs.

APPENDIX A

Combined Data for Physical and Chemical Variables Obtained from 15 Lakes in the Scottie-Desper Creeks Study Area and the Factor Loadings for Selected Variables Used in the Principal Components Analyses.

Appendix Table A-1. Combined data for physical and chemical variables obtained from 15 lakes and two creeks during spring (19 June - 4 July) and fall (29 August - 11 September), Scottie-Desper Creeks Study Area, Alaska, 1979.

Lake No.	Water transparency rank (1=low)	Temperature (°C)	Maximum depth (m)	Area (ha)	pH	Total alkalinity $mgCaCO_3 \cdot liter^{-1}$	Total hardness $mgCaCO_3 \cdot liter^{-1}$	Silicon ug-atoms $\cdot liter^{-1}$	Reactive phosphorus ug-atoms $\cdot liter^{-1}$	Nitrate ug-atoms $\cdot liter^{-1}$	Nitrite ug-atoms $\cdot liter^{-1}$	Ammonia ug-atoms $\cdot liter^{-1}$	Combined nitrogen ug-atoms $\cdot liter^{-1}$
10	2	14.6	1.6	8.3	7.2	84	84	26.85	0.60	4.92	1.38	5.18	11.48
17	3	13.3	10.4	26.9	7.4	148	148	72.83	0.64	2.97	0.52	4.48	7.96
1	1	13.8	4.2	72.8	7.4	50	56	13.37	0.54	0.60	0.22	4.56	5.38
7	1	14.0	1.0	4.4	7.4	89	84	18.02	0.75	0.58	0.29	5.75	6.60
9	1	13.8	2.3	20.2	7.7	71	71	12.94	0.83	0.83	0.28	3.28	4.40
15	2	11.6	2.5	53.9	7.5	72	72	35.60	0.40	3.18	0.32	3.63	7.12
16	2	12.2	1.5	76.1	7.4	145	145	67.10	0.83	3.24	0.38	4.40	8.02
35	1	14.2	2.5	4.9	7.3	66	67	31.58	0.78	2.94	0.46	5.53	8.93
42	1	14.3	2.0	3.9	8.1	77	86	20.34	0.54	0.14	0.22	2.52	2.88
19	3	12.4	2.0	3.3	7.0	50	44	24.48	0.19	1.54	0.12	2.84	4.38
41	2	15.3	1.1	0.5	7.0	45	42	12.06	0.18	0.55	0.20	2.97	3.70
44	3	13.6	3.5	9.1	6.9	26	15	8.54	0.12	0.19	0.16	2.85	3.20
47	3	16.8	4.4	5.7	6.6	20	16	29.91	0.25	2.22	0.16	2.56	4.78
49	2	17.2	2.3	52.6	7.1	26	16	18.40	0.22	1.63	0.14	3.58	5.25
50	3	17.2	1.5	11.1	7.5	46	44	21.65	0.22	2.22	0.18	2.64	5.04
Scottie Cr.	-	6.9	-	-	7.2	44	52	32.15	0.29	3.80	0.30	3.00	7.10
Desper Cr.	-	8.4	-	-	7.0	45	49	40.15	0.29	2.23	0.16	2.69	5.08

Appendix Table A-2. Factor loadings for physical and chemical variables used in the principal component analysis (Figure 6).

Variable	Component 1	Component 2	Component 3
Temperature	-0.577	-0.337	0.050
pH	0.818	-0.124	-0.172
Alkalinity	0.723	0.558	0.293
Hardness	0.761	0.529	0.277
Depth	-0.080	0.778	0.038
Area	0.288	0.454	-0.141
Nitrite	0.192	0.013	0.904
Nitrate	-0.011	0.392	0.825
Phosphate	0.850	0.083	0.334
Ammonia	0.495	0.038	0.629
Silicon	0.278	0.865	0.294

APPENDIX B

Supporting Information on Taxa and Functional Group Designations Used in This Study and Summaries of Gut Analyses of Selected Taxa.

Appendix Table B-1. List of invertebrate taxa from Lakes 10 and 17, Scottie-Desper Creeks Study Area, Alaska, 1979.

PHYLUM COELENTERATA
- Class Hydrazoa (hydras)

PHYLUM PLATYHELMINTHES (flatworms)
- Class Turbellaria

PHYLUM NEMATODA (roundworms)

PHYLUM ANNELIDA
- Class Oligochaeta (earthworms)
- Class Hirudinea (leeches)

PHYLUM MOLLUSCA
- Class Gastropoda
  - Order Basommatophora
    - Family Lymnaeidae (pond snails)
    - Family Planorbidae (orb snails)
  - Order Mesogastropoda
    - Family Valvatidae (round-mouthed snails)
    - Family Sphaeriidae (fingernail clams)

PHYLUM ARTHROPODA
- Class Insecta
  - Order Ephemeroptera (mayflies)
    - Family Baetidae*
  - Order Odonata
    - Suborder Zygoptera (damselflies)
      - Family Coenagroinidae*
      - Family Lestidae*
    - Suborder Anisoptera (dragonflies)
      - Family Aeshnidae*
      - Family Libellulidae
  - Order Hemiptera
    - Family Corixidae (water boatmen)
  - Order Trichoptera (caddisflies)
    - Family Leptoceridae**
    - Family Limnephilidae*
      - Genus Limnephilus
    - Family Phryganeidae
      - Genus Anabolia
    - Family Polycentropodidae*
      - Genus Polycentropus
  - Order Lepidoptera** (aquatic caterpillars)

* Present only in Lake 10.
** Present only in Lake 17.

Appendix Table B-1 (Continued).

- Order Coleoptera
  - Family Dytiscidae* (diving beetles)
  - Family Gyrinidae* (whirligig beetles)
  - Family Haliplidae* (crawling beetles)
- Order Diptera
  - Family Ceratopogonidae (no-see-ums)
  - Family Chaoboridae (phantom midges)
  - Family Chironomidae*** (midges)
    - Subfamily Chironominae
      - Tribe Chironomini
        - Genus Chironomus
        - Genus Cryptochironomus
        - Genus Glyptotendipes
        - Genus Polypedilum
        - Genus Dicrotendipes
        - Genus Cladopelma
      - Tribe Tanytarsini
    - Subfamily Tanypodinae
      - Tribe Tanypodini
        - Genus Tanypus
      - Tribe Macropelopiini
        - Genus Procladius
        - Genus Derotanypus
    - Subfamily Orthocladiinae
      - Genus Cricotopus
- Class Crustacea
  - Order Conchostraca* (clam shrimps)
  - Order Cladocera (water fleas)
  - Order Ostracoda (seed shrimps)
  - Order Eucopepoda (copepods)
    - Suborder Calanoida
    - Suborder Cyclopoida
    - Suborder Harpacticoida*
  - Order Amphipoda (scuds)
    - Family Talitridae
      - Genus Hyalella
    - Family Gammaridae
- Class Arachnoidea
  - Order "Hydracarina" (water mites)

* Present only in Lake 10.
** Present only in Lake 17.
*** Due to taxonomic difficulties, chironomids in Lake 10 were only keyed to subfamilies Chironominae and Tanypodinae.

Appendix Table B-2. Taxa and functional group designations used in volumetric analyses for Lakes 10 and 17, Scottie-Desper Creeks Study Area, Alaska, 1979. Sources are listed in order of priority; POM refers to particulate organic matter.

Taxon	Functional Group	Principal source(s) for designation[1]
Hydrazoa	Engulfer-predator	1
Oligochaeta	Collector-gatherer-POM	1
Hirudinea	Non-engulfer-predator	1
Planorbidae	Scraper	1
Valvatidae	Scraper	1
Sphaeriidae	Collector-filterer	1
Amphipoda	Collector-gatherer-algae	1
Hyalella	Collector-gatherer-algae	1
Gammaridae	Collector-gatherer-algae	1
Hydracarina	Non-engulfer-predator	1
Ostracoda	Collector-gatherer-POM	1
Conchostraca	collector-gatherer-POM	1
Odonata	Engulfer-predator	2
Lestidae	Engulfer-predator	2
Coenagroinidae	Engulfer-predator	2
Phryganeidae	Shredder	3, 2
Limnephilidae	Shredder	3, 2
Dytiscidae	Non-engulfer-predator	2
Gyrinidae	Engulfer-predator	2
Ceratopogonidae	Insufficient volume	2
Corixidae	Non-engulfer-predator	2
Chaoboridae	Engulfer-predator	2
Chironomus	Collector-gatherer-POM	3, 2
Cryptochironomus	Engulfer-predator	3, 2
Dicrotendipes	Collector-gatherer-POM	3, 2
Glyptotendipes	Collector-gatherer-POM	3, 2
Polypedilum	Collector-gatherer-POM	3, 2
Procladius	Collector-gatherer-algae	3, 2
Tanypus	Collector-gatherer-algae	3, 2
Tanytarsini	Collector-gatherer-POM	3, 2
Cricotopus	Collector-gatherer-algae	
Tanypodinae	Collector-gatherer-POM	3, 2
Chironominae	Collector-gatherer-POM	3, 2
Other Chironomidae	Collector-gatherer-POM	3

[1]Derived from Pennak (1978).
[2]Derived from Merritt and Cummins (1978).
[3]Derived from gut analyses.

Appendix Table B-3. Summary of food types present in guts of larval Chironomidae obtained during late spring (19 June - 4 July, 1979) in Lake 17, Scottie-Desper Creeks Study Area, Alaska.

Taxon	Stratum	Food types				Sample Size	Functional Group
		CPOM	FPOM	Algae	Animal		
Chironomus	≤ 1.0m	50%	38%	12%	--	2	Collector-gatherer-POM
	> 1.0m	Present (4)	69%	31%	--	4	Collector-gatherer-POM
Glyptotendipes (shallow only)	≤ 1.0m	45%	40%	15%	--	5	Collector-gatherer-POM
Tanypus	≤ 1.0m	--	12%	88%	--	2	Collector-gatherer-algae
	> 1.0m	--	15%	85%	Present (1)	5	Collector-gatherer-algae
Procladius	≤ 1.0m	6%	31%	63%	--	4	Collector-gatherer-algae
	> 1.0m	--	59%	8%	33%	3	Collector-gatherer-algae
Tanytarsini	≤ 1.0m	--	75%	25%	--	1	Collector-gatherer-POM
	> 1.0m	Present (1)	79%	21%	--	6	Collector-gatherer-POM
Cricotopus (shallow only)	≤ 1.0m	Present (1)	38%	62%	--	4	Collector-gatherer-algae
Polypedilum (shallow only)	≤ 1.0m	Present (1)	80%	10%	10%	5	Collector-gatherer-POM
Total Chironomidae	≤ 1.0m	15%	46%	37%	2%	23	Collector-gatherer
Total Chironomidae	> 1.0m	Present (4)	56%	39%	5%	18	Collector-gatherer

Appendix Table B-4. Summary of food types present in guts of larval Chironomidae obtained during fall (29 August - 11 September, 1979) in Lake 17, Scottie-Desper Creeks Study Area, Alaska.

Taxon	Stratum	Food types				Sample Size	Functional Group
		CPOM	FPOM	Algae	Animal		
Chironomus	≤ 1.0m	Present (4)	100%	Present (5)	--	5	Collector-gatherer-POM
	> 1.0m	Present (2)	75%	25%	--	3	Collector-gatherer-POM
Glyptotendipes	≤ 1.0m	Present (2)	88%	12%	--	2	Collector-gatherer-POM
	> 1.0m	--	63%	25%	--	2	Collector-gatherer-POM
Tanypus	≤ 1.0m	--	12%	88%	--	2	Collector-gatherer-algae
	> 1.0m	--	50%	50%	--	1	Collector-gatherer-algae
Procladius	≤ 1.0m	--	25%	75%	--	1	Collector-gatherer-algae
	> 1.0m	--	25%	75%	--	2	Collector-gatherer-algae
Dicrotendipes (shallow only)	≤ 1.0m	Present (1)	100%	Present (3)	--	3	Collector-gatherer-POM
Tanytarsini (shallow only)	≤ 1.0m	--	100%	Present (2)	Present (1)	2	Collector-gatherer-POM
Cryptochronomus[1] (Deep only)	> 1.0m	--	75%	--	25%	2	Engulfer-predator
Derotanypus (shallow only)	≤ 1.0m	Present (2)	85%	15%	Present (2)	5	Collector-gatherer-POM

[1] Designation of Engulfer-predator by Merritt and Cummins (1978) and presence of significant amounts of animal matter were the basis of the functional group determination.

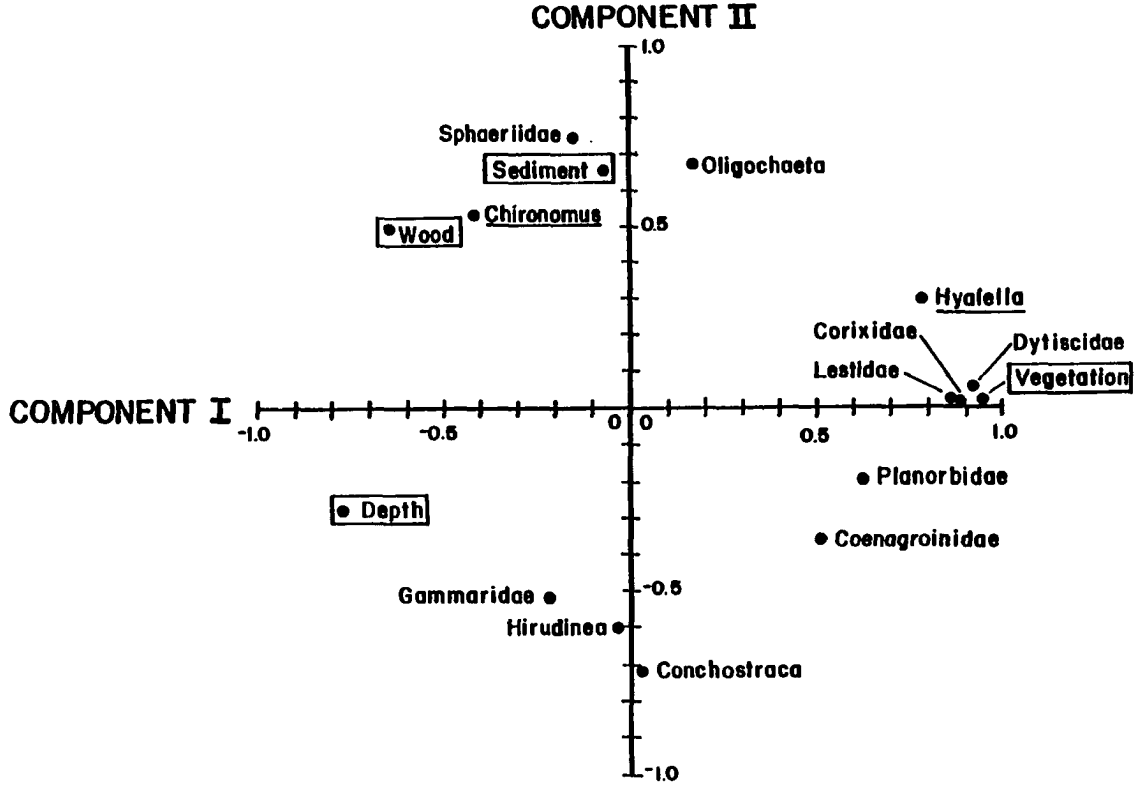
Appendix Table B-5. Summary of food types present in guts of larval Chironomidae and Trichoptera obtained during spring (19 June - 4 July) fall (29 August - 11 September, 1979) in Lake 10 of Scottie-Desper Creeks Study Area, Alaska.

Taxon	Stratum	Season	Food types				Sample Size	Functional Group
			CPOM	FPOM	Algae	Animal		
Chironomus	≤ 1.0m	Spring	Present (2)	81%	12%	7%	4	Collector-gatherer-POM
	> 1.0m	Spring	--	88%	12%	Present (1)	4	Collector-gatherer-POM
Tanypodinae	≤ 1.0m	Spring	--	88%	12%	--	2	Collector-gatherer-POM
	> 1.0m	Spring	--	65%	5%	30%	5	Collector-gatherer-POM
Other Chironomidae (shallow only)	≤ 1.0m	Spring	Present (3)	88%	12%	--	4	Collector-gatherer-POM
Total Chironomidae	≤ 1.0m	Spring	Present (5)	85%	12%	3%	10	Collector-gatherer
	> 1.0m	Spring	--	75%	8%	17%	9	Collector-gatherer
Chironomus	> 1.0m	Fall	50%	50%	Present (2)	Present (2)	2	Collector-gatherer-POM
Other Chironomidae (shallow only)	≤ 1.0m	Fall	Present (2)	100%	Present (3)	Present (1)	3	Collector-gatherer-POM
	> 1.0m	Fall	--	100%	--	--	5	Collector-gatherer-POM
Total Chironomidae	≤ 1.0m	Fall	14%	85%	--	Present (2)	7	Collector-gatherer
Total Chironomidae	> 1.0m	Fall	Present (2)	100%	Present (3)	Present (1)	3	Collector-gatherer
Limnephilus[1]	≤ 1.0m	Spring	100%	Present (2)	--	--	2	Shredder
Anabolia[2]	≤ 1.0m	Spring	--	50%	--	50%	1	Shredder
Phryganeidae[3]	≤ 1.0m	Fall	--	100%	--	Present (2)	2	Shredder

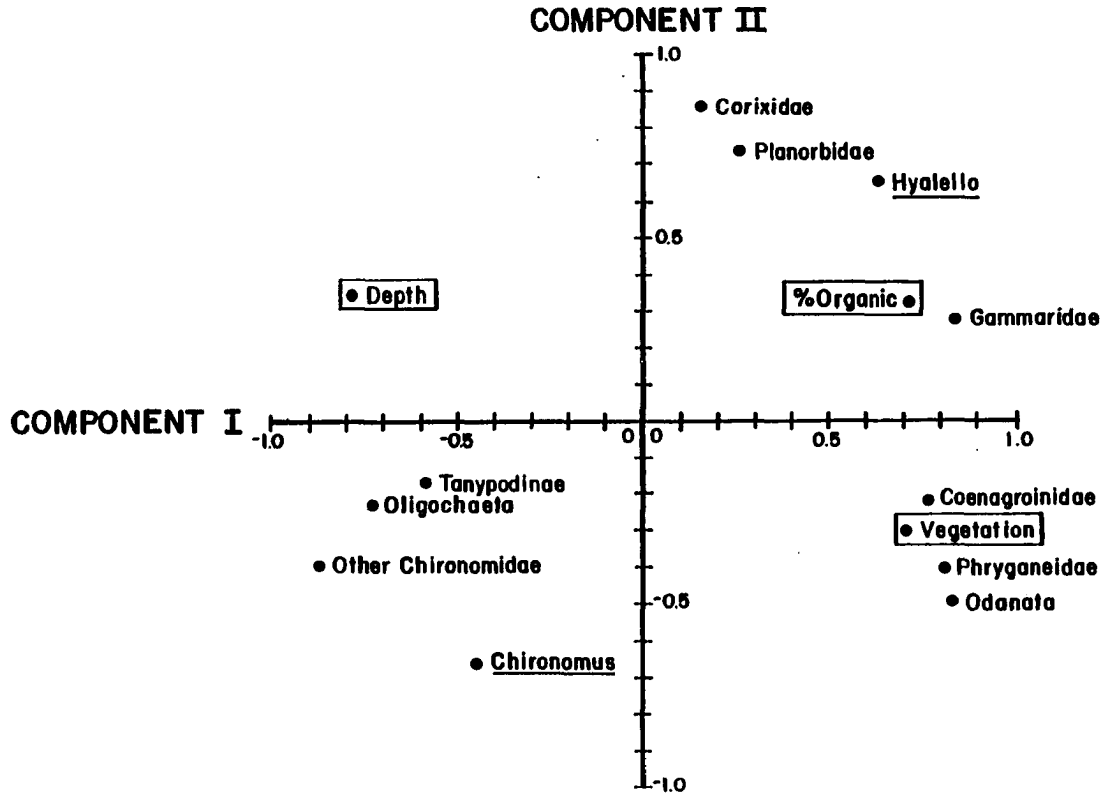
[1]Gut materials were generally 0.5-1.0 mm in diameter.
[2]Guts were empty in two of three larvae sampled: functional group was assumed.
[3]One hundred percent of material was ≤ 0.5 mm in diameter; 75% of material was ≤ 0.3 mm in diameter.

APPENDIX C

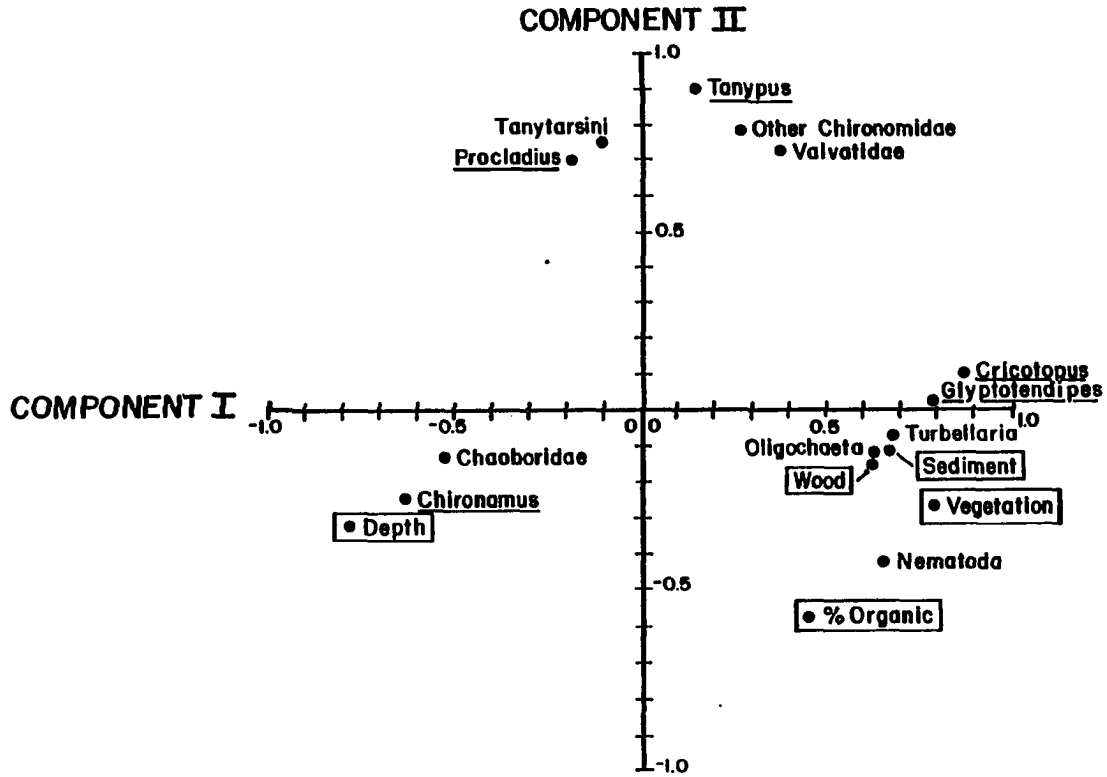
Ordinations of Environmental and Taxonomic Variables of Volumetric Data of Benthic Macroinvertebrates in Lakes 10 and 17 and Lists of Variables Factor Loadings for all Principal Components Analyses Used in the Benthic Macroinvertebrate Study.



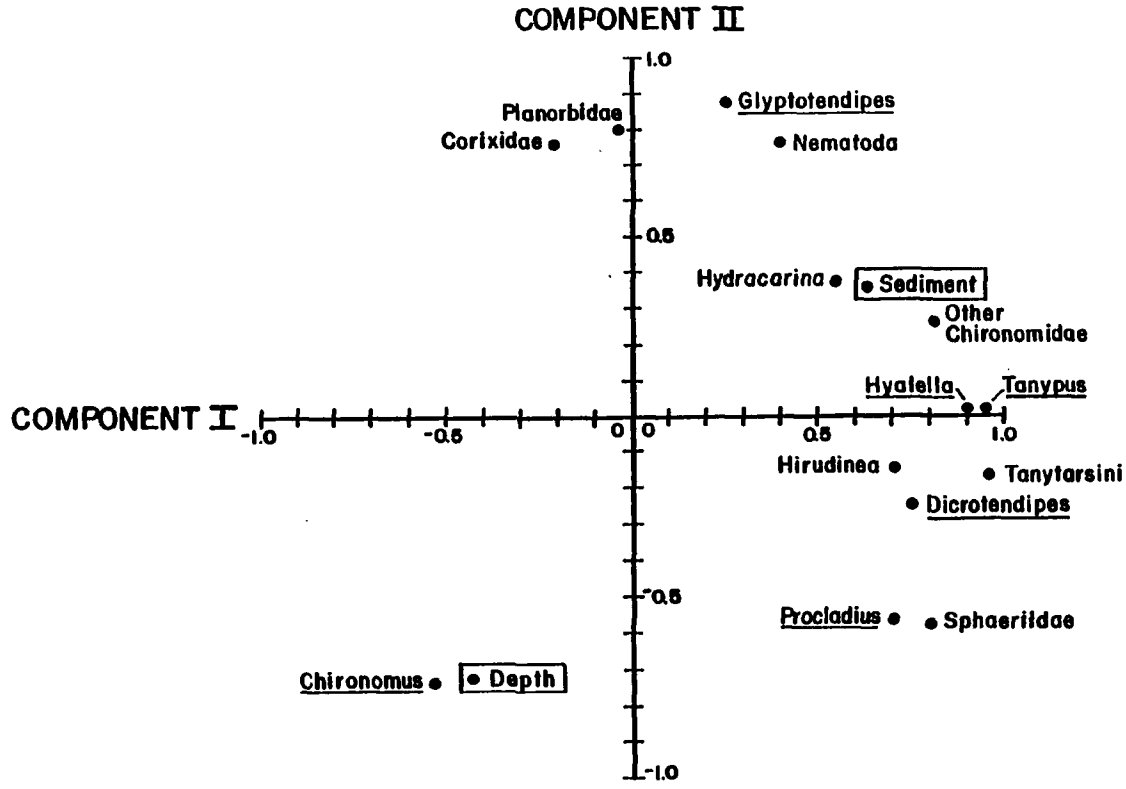
Appendix Figure C-1. Ordination of environmental and taxonomic variables for spring/volumetric data for Lake 10, Scottie-Desper Creeks Study Area, Alaska, 1979. Forty-seven percent of total variation was accounted for on Components I and II (29% and 18%, respectively).



Appendix Figure C-2. Ordination of environmental and taxonomic variables for fall/volumetric data for Lake 10, Scottie-Desper Creeks Study Area, Alaska, 1979. Fifty-five percent of total variation was accounted for on Components I and II (35% and 20%, respectively).



Appendix Figure C-3. Ordination of environmental and taxonomic variables for spring/volumetric data for Lake 10, Scottie-Desper Creeks Study Area, Alaska, 1979. Fifty-four percent of total variation was accounted for on Components I and II (33% and 21%, respectively).



Appendix Figure C-4. Ordination of environmental and taxonomic variables for fall/volumetric data for Lake 10, Scottie-Desper Creeks Study Area, Alaska, 1979. Fifty-five percent of total variation was accounted for on Components I and II (32% and 23%, respectively).

Appendix Table C-1. List of variables used in principal component analyses in Lakes 10 and 17, Scottie-Desper Creeks Study Area, Alaska, 1979.

	Lake 10	Lake 17
	Depth (water)	Depth (water)
	Sediment (dry wt)	Sediment (dry wt)
	Wood (dry wt)	Wood (dry wt)
	Vegetation (dry wt)	Vegetation (dry wt)
1, [3]	% Organic (substrate)	% organic (substrate)
1, [3]	Oligochaeta	Oligochaeta
3, [4]	Hirudinea	Hirudinea
2, [4]	Turbellaria	Turbellaria
2, [4]	Hydrazoa	Hydrazoa
	Nematoda	Nematoda
	Planorbidae	Planorbidae
	Valvatidae	Valvatidae
	Sphaeriidae	Sphaeriidae
	Hyalella	Hyalella
3, [4]	Gammaridae	Gammaridae
2, [4]	Amphipoda	Hydracarina
2, [4]	Hydracarina	Ostracoda
	Ostracoda	Ceratopogonidae
3, [4]	Conchostraca	Corixidae
	Lestidae	Chaoboridae
1, [2]	Coenagroinidae	Chironomus
3, [4]	Odonata	Cryptochironomus
1, [2]	Limnephilidae	Glyptotendipes
	Phryganeidae	Polypedilum
	Dytiscidae	Dicrotendipes
2, 3, [4]	Gyrinidae	Tanypus
	Corixidae	Procladius
2, [4]	Ceratopogonidae	Tanytarsini
	Chaoboridae	Cricotopus
	Chironomus	Cladopelma
	Tanypodinae	Other Chironomidae
	Other Chironomidae	

[1]Not used in analysis of spring/numerical data.
[2]Not used in analysis of spring/volumetric data.
[3]Not used in analysis of fall/numerical data.
[4]Not used in analysis of fall/volumetric data.

Appendix Table C-2. Factor loadings for environmental and taxonomic variables for spring/numerical data, Lake 10, Scottie-Desper Creeks Study Area, Alaska, 1979.

	Variable	Component I	Component II	Component III
	Depth (water)	-0.704	-0.436	0.307
	Sediment (dry wt)	-0.157	0.393	0.386
	Wood (dry wt)	-0.614	0.050	0.136
	Vegetation (dry wt)	0.930	-0.117	0.219
1, [3]	% Organic (substrate)	0.278	0.411	0.718
1, [3]	Oligochaeta	--	--	--
3, [4]	Hirudinea	0.782	-0.317	-0.068
2, [4]	Turbellaria	0.811	0.285	0.205
2, [4]	Hydrazoa	0.554	-0.404	0.456
2, [4]	Nematoda	-0.167	0.409	-0.203
	Planorbidae	0.777	-0.329	-0.142
	Valvatidae	-0.462	-0.327	0.687
	Sphaeriidae	-0.141	0.742	-0.262
	Hyalella	0.929	-0.122	-0.074
3, [4]	Gammaridae	-0.182	-0.411	0.309
2, [4]	Amphipoda	0.907	-0.020	0.103
2, [4]	Hydracarina	0.202	0.140	0.124
2, [4]	Ostracoda	-0.186	-0.273	0.757
3, [4]	Conchostraca	0.237	-0.472	-0.398
3, [4]	Lestidae	0.897	-0.246	-0.071
1, [2]	Coenagroinidae	0.880	-0.127	0.227
1, [2]	Odonata	--	--	--
3, [4]	Limnephilidae	0.435	0.827	0.210
1, [2]	Phryganeidae	--	--	--
2, 3, [4]	Dytiscidae	0.927	-0.242	0.023
	Gyrinidae	0.172	0.240	0.499
2, [4]	Corixidae	0.785	-0.110	-0.298
[2]	Ceratopogonidae	0.132	0.850	-0.012
[2]	Chaoboridae	-0.443	-0.273	0.685
	Chironomus	-0.357	-0.192	-0.573
	Tanypodinae	-0.261	-0.114	-0.544
	Other Chironomidae	0.337	0.882	0.119

[1]Not used in analysis of spring/numerical data.
[2]Not used in analysis of spring/volumetric data.
[3]Not used in analysis of fall/numerical data.
[4]Not used in analysis of fall/volumetric data.

Appendix Table C-3. Factor loadings for environmental and taxonomic variables for fall/numerical data, Lake 10, Scottie-Desper Creeks Study Area, Alaska, 1979.

	Variable	Component I	Component II	Component III
	Depth (water)	-0.905	0.021	-0.031
	Sediment (dry wt)	-0.405	0.553	-0.144
	Wood (dry wt)	0.349	0.632	-0.282
	Vegetation (dry wt)	0.762	0.039	0.225
1, 3	% Organic (substrate)	0.600	-0.488	0.226
1, 3	Oligochaeta	--	--	--
3, 4	Hirudinea	0.764	-0.576	-0.106
2, 4	Turbellaria	--	--	--
2, 4	Hydrazoa	-0.107	-0.414	0.784
2, 4	Nematoda	-0.557	-0.352	0.448
	Planorbidae	0.497	0.621	0.068
	Valvatidae	0.036	0.348	0.825
	Sphaeriidae	0.520	0.670	0.184
	Hyalella	0.720	-0.610	-0.133
3, 4	Gammaridae	0.812	-0.392	-0.185
2, 4	Amphipoda	--	--	--
2, 4	Hydracarina	-0.363	-0.127	-0.565
2, 4	Ostracoda	0.232	0.595	0.202
3, 4	Conchostraca	0.493	0.700	-0.021
3, 4	Lestidae	--	--	--
1, 2	Coenagroinidae	0.799	0.101	-0.267
1, 2	Odonata	0.721	0.468	0.183
3, 4	Limnephilidae	--	--	--
1, 2	Phryganeidae	0.902	0.149	-0.016
4	Dytiscidae	0.654	-0.636	-0.306
2, 3, 4	Gyrinidae	--	--	--
2, 4	Corixidae	0.167	-0.764	0.541
2, 4	Ceratopogonidae	-0.087	-0.210	-0.288
2	Chaoboridae	-0.386	-0.111	-0.553
	Chironomus	0.012	0.787	0.087
	Tanypodinae	-0.546	0.216	-0.090
	Other Chironomidae	0.975	0.085	-0.122

[1]Not used in analysis of spring/numerical data.
[2]Not used in analysis of spring/volumetric data.
[3]Not used in analysis of fall/numerical data.
[4]Not used in analysis of fall/volumetric data.

Appendix Table C-4. Factor loadings for environmental and taxonomic variables for spring/numerical data, Lake 17, Scottie-Desper Creeks Study Area, Alaska, 1979

	Variable	Component I	Component II	Component III
	Depth (water)	-0.844	0.479	-0.053
	Sediment (dry wt)	0.673	-0.289	-0.085
	Wood (dry wt)	0.634	0.195	0.485
	Vegetation (dry wt)	0.719	0.134	0.396
	% Organic (substrate)	0.277	0.515	0.180
1, [3]	Oligochaeta	--	--	--
1, [2]	Hirudinea	--	--	--
3, [4]	Turbellaria	0.792	-0.275	-0.005
1, [2]	Hydrazoa	--	--	--
1, [2]	Nematoda	0.779	-0.570	-0.186
	Planorbidae	--	--	--
	Valvatidae	0.621	0.318	0.478
1, [2]	Sphaeriidae	-0.519	-0.165	0.637
1, [2]	Hyalella	--	--	--
	Gammaridae	--	--	--
2, [4]	Hydracarina	-0.419	0.646	-0.446
	Ostracoda	0.623	0.014	-0.211
	Ceratopogonidae	0.245	-0.283	0.208
	Corixodae	0.828	0.393	0.113
	Chaoboridae	-0.724	0.481	0.188
1, [2]	Chironomus	-0.616	-0.091	0.373
	Cryptochironomus	--	--	--
3, [4]	Glyptotendipes	0.731	0.491	0.358
1, [2]	Polypedilum	0.479	0.381	-0.175
	Dicrotendipes	--	--	--
	Tanypus	-0.439	0.207	-0.269
	Procladius	-0.683	-0.201	0.566
3, [4]	Tanytarsini	-0.523	-0.030	0.669
2, [4]	Cricotopus	0.677	0.530	0.176
	Cladopelma	-0.047	-0.460	-0.275
	Other Chironomidae	-0.085	0.862	-0.332

[1]Not used in analysis of spring/numerical data.
[2]Not used in analysis of spring/volumetric data.
[3]Not used in analysis of fall/numerical data.
[4]Not used in analysis of fall/volumetric data.

Appendix Table C-5. Factor loadings for environmental and taxonomic variables for fall/numerical data, Lake 17, Scottie-Desper Creeks Study Area, Alaska, 1979

	Variable	Component I	Component II	Component III
	Depth (water)	-0.828	0.413	-0.011
	Sediment (dry wt)	0.112	-0.269	0.352
	Wood (dry wt)	0.838	0.466	-0.062
	Vegetation (dry wt)	0.792	0.578	-0.075
1, [3]	% Organic (substrate)	0.301	0.750	0.391
1, [3]	Oligochaeta	--	--	--
1, [2]	Hirudinea	0.809	0.215	0.300
3, [4]	Turbellaria	--	--	--
1, [2]	Hydrazoa	0.648	0.110	-0.116
1, [2]	Nematoda	-0.041	0.795	0.257
	Planorbidae	0.246	-0.566	-0.246
	Valvatidae	0.110	-0.516	-0.083
1, [2]	Sphaeriidae	-0.590	0.247	-0.380
1, [2]	Hyalella	0.760	0.567	-0.141
	[2] Gammaridae	0.787	0.574	-0.122
2, [4]	Hydracarina	-0.232	0.054	0.804
	Ostracoda	0.201	-0.814	-0.359
	[2] Ceratopogonidae	-0.301	0.324	0.670
	[4] Corixodae	0.845	0.370	-0.247
	[4] Chaoboridae	-0.301	0.324	0.670
1, [2]	Chironomus	-0.768	0.512	-0.122
	Cryptochironomus	-0.633	0.319	-0.496
3, [4]	Glyptotendipes	0.812	0.112	-0.256
1, [2]	Polypedilum	--	--	--
	Dicrotendipes	0.245	-0.336	0.565
	Tanypus	0.111	-0.361	0.756
	Procladius	-0.737	0.553	-0.070
3, [4]	Tanytarsini	-0.022	-0.618	0.092
2, [4]	Cricotopus	--	--	--
	Cladopelma	-0.400	0.195	-0.506
	Other Chironomidae	0.332	-0.901	0.096

[1] Not used in analysis of spring/numerical data.
[2] Not used in analysis of spring/volumetric data.
[3] Not used in analysis of fall/numerical data.
[4] Not used in analysis of fall/volumetric data.

Appendix Table C-6. Factor loadings for environmental and taxonomic variables for spring/volumetric data, Lake 10, Scottie-Desper Creeks Study Area, Alaska, 1979.

	Variable	Component I	Component II	Component III
	Depth (water)	-0.767	-0.285	-0.211
	Sediment (dry wt)	-0.080	0.661	0.029
	Wood (dry wt)	-0.651	0.505	-0.243
	Vegetation (dry wt)	0.934	-0.008	-0.105
1, 3	% Organic (substrate)	0.283	-0.074	0.687
1, 3	Oligochaeta	0.175	0.671	-0.527
3, 4	Hirudinea	-0.033	-0.599	-0.105
2, 4	Turbellaria	0.251	0.382	0.761
2, 4	Hydrazoa	--	--	--
2, 4	Nematoda	--	--	--
	Planorbidae	0.625	-0.192	-0.290
	Valvatidae	-0.476	-0.257	0.136
	Sphaeriidae	-0.159	0.755	0.433
	Hyalella	0.786	0.302	-0.247
3, 4	Gammaridae	-0.217	-0.523	-0.222
2, 4	Amphipoda	0.418	0.496	-0.385
2, 4	Hydracarina	--	--	--
2, 4	Ostracoda	--	--	--
3, 4	Conchostraca	0.049	-0.716	0.022
	Lestidae	0.893	-0.010	-0.145
1, 2	Coenagroinidae	0.501	-0.367	0.147
3, 4	Odonata	--	--	--
1, 2	Limnephilidae	0.412	0.084	0.141
4	Phryganeidae	--	--	--
2, 3, 4	Dytiscidae	0.905	0.056	-0.052
	Gyrinidae	--	--	--
2, 4	Corixidae	0.870	-0.040	-0.232
2	Ceratopogonidae	--	--	--
2	Chaoboridae	--	--	--
	Chironomus	-0.438	0.530	-0.619
	Tanypodinae	-0.328	0.215	-0.252
	Other Chironomidae	-0.003	0.391	0.837

[1]Not used in analysis of spring/numerical data.
[2]Not used in analysis of spring/volumetric data.
[3]Not used in analysis of fall/numerical data.
[4]Not used in analysis of fall/volumetric data.

Appendix Table C-7. Factor loadings for environmental and taxonomic variables for fall/volumetric data, Lake 10, Scottie-Desper Creeks Study Area, Alaska, 1979.

	Variable	Component I	Component II	Component III
	Depth (water)	-0.796	0.350	0.154
	Sediment (dry wt)	-0.496	-0.424	0.282
	Wood (dry wt)	0.280	-0.445	0.747
	Vegetation (dry wt)	0.711	-0.308	-0.537
1, 3	% Organic (substrate)	0.735	0.310	-0.446
1, 3	Oligochaeta	-0.724	-0.235	0.046
3, 4	Hirudinea	-0.165	0.008	0.218
2, 4	Turbellaria	--	--	--
2, 4	Hydrazoa	--	--	--
2, 4	Nematoda	--	--	--
	Planorbidae	0.269	0.726	-0.074
	Valvatidae	-0.359	-0.086	-0.189
	Sphaeriidae	-0.224	-0.426	-0.617
	Hyalella	0.638	0.655	0.078
3, 4	Gammaridae	0.831	0.258	0.304
2, 4	Amphipoda	--	--	--
2, 4	Hydracarina	--	--	--
2, 4	Ostracoda	--	--	--
3, 4	Conchostraca	0.281	-0.474	0.416
3, 4	Lestidae	--	--	--
1, 2	Coenagroinidae	0.760	-0.238	0.470
3, 4	Odonata	0.829	-0.494	0.026
1, 2	Limnephilidae	--	--	--
4	Phryganeidae	0.817	-0.404	-0.353
2, 3, 4	Dytiscidae	--	--	--
	Gyrinidae	--	--	--
2, 4	Corixidae	0.148	0.856	-0.237
	Ceratopogonidae	--	--	--
2	Chaoboridae	-0.366	0.196	0.251
	Chironomus	-0.457	-0.671	-0.368
	Tanypodinae	-0.605	-0.189	-0.333
	Other Chironomidae	0.891	-0.405	-0.118

[1]Not used in analysis of spring/numerical data.
[2]Not used in analysis of spring/volumetric data.
[3]Not used in analysis of fall/numerical data.
[4]Not used in analysis of fall/volumetric data.

Appendix Table C-8. Factor loadings for environmental and taxonomic variables for spring/volumetric data, Lake 17, Scottie-Desper Creeks Study Area, Alaska, 1979

Variable	Component I	Component II	Component III
Depth (water)	-0.764	-0.308	-0.249
Sediment (dry wt)	0.680	-0.114	0.224
Wood (dry wt)	0.625	-0.160	-0.634
Vegetation (dry wt)	0.793	-0.264	-0.398
[1, 3]% Organic (substrate)	0.466	-0.585	-0.166
[1, 3]Oligochaeta	0.622	-0.192	0.699
[1, 2]Hirudinea	--	--	--
[3, 4]Turbellaria	0.697	-0.071	0.603
[1, 2]Hydrazoa	--	--	--
[1, 2]Nematoda	0.655	-0.412	0.488
[1, 2]Planorbidae	--	--	--
Valvatidae	0.393	0.722	-0.512
[1, 2]Sphaeriidae	-0.437	-0.115	-0.258
[1, 2]Hyalella	--	--	--
[2]Gammaridae	--	--	--
[2, 4]Hydracarina	--	--	--
[2, 4]Ostracoda	--	--	--
[2]Ceratopogonidae	--	--	--
[4]Corixodae	--	--	--
[4]Chaoboridae	-0.510	-0.138	-0.178
[1, 2]Chironomus	-0.628	-0.249	0.218
[2]Cryptochironomus	--	--	--
[3, 4]Glyptotendipes	0.770	0.017	-0.581
[1, 2]Polypedilum	0.453	0.168	0.422
[2]Dicrotendipes	--	--	--
Tanypus	0.154	0.903	0.187
Procladius	-0.194	0.769	0.243
[3, 4]Tanytarsini	-0.115	0.740	0.189
[2, 4]Cricotopus	0.864	0.105	-0.289
[4]Cladopelma	--	--	--
Other Chironomidae	0.278	0.785	-0.169

[1]Not used in analysis of spring/numerical data.
[2]Not used in analysis of spring/volumetric data.
[3]Not used in analysis of fall/numerical data.
[4]Not used in analysis of fall/volumetric data.

Appendix Table C-9. Factor loadings for environmental and taxonomic variables for fall/volumetric data, Lake 17, Scottie-Desper Creeks Study Area, Alaska, 1979

Variable	Component I	Component II	Component III
Depth (water)	-0.405	-0.826	-0.314
Sediment (dry wt)	0.625	-0.356	0.373
Wood (dry wt)	-0.092	0.440	0.782
Vegetation (dry wt)	-0.220	0.393	0.793
[1, 3]% Organic (substrate)	-0.260	-0.212	0.841
[1, 3]Oligochaeta	-0.089	-0.158	-0.395
[1, 2]Hirudinea	0.711	-0.147	0.579
[3, 4]Turbellaria	--	--	--
[1, 2]Hydrazoa	0.401	0.033	-0.284
[1, 2]Nematoda	0.408	0.748	-0.478
[1, 2]Planorbidae	-0.029	0.777	-0.313
Valvatidae	0.495	0.416	-0.431
[1, 2]Sphaeriidae	0.807	-0.571	0.004
[1, 2]Hyalella	0.905	0.011	0.316
[1, 2]Gammaridae	-0.216	0.405	0.780
[2, 4]Hydracarina	0.543	0.378	-0.489
[2, 4]Ostracoda	--	--	--
[2]Ceratopogonidae	--	--	--
[4]Corixodae	-0.220	0.757	0.005
[4]Chaoboridae	--	--	--
[1, 2]Chironomus	-0.534	-0.733	-0.325
[1, 2]Cryptochironomus	-0.478	-0.111	-0.322
[3, 4]Glyptotendipes	0.240	0.877	-0.146
[1, 2]Polypedilum	--	--	--
[1, 2]Dicrotendipes	0.743	-0.263	0.393
Tanypus	0.957	-0.044	0.054
Procladius	0.699	-0.572	-0.275
[3, 4]Tanytarsini	0.944	-0.189	0.174
[2, 4]Cricotopus	--	--	--
[2, 4]Cladopelma	--	--	--
Other Chironomidae	0.801	0.260	-0.362

[1]Not used in analysis of spring/numerical data.
[2]Not used in analysis of spring/volumetric data.
[3]Not used in analysis of fall/numerical data.
[4]Not used in analysis of fall/volumetric data.

REFERENCES CITED

Ager, T.A. 1975. Late quaternary environmental history of the Tanana Valley, Alaska. Institute of Polar Studies Report No. 54, Univ. Ohio 117 p.

Alexander, V., and R.J. Barsdate. 1971. Physical limnology, chemistry and plant productivity of a taiga lake. Int. Rev. gesamten Hydrobiol. 56:825-872.

_____. and R.J. Barsdate. 1974. Limnological studies of a subarctic lake system. Int. Rev. gesamten Hydrobiol. 59:737-753.

Alt, K.T. 1979. Contributions to the life history of the humpback whitefish in Alaska. Trans. Am. Fish. Soc. 108:156-160.

Ayles, H.A. 1976. Lake whitefish (Coregonus clupeaformis (Mitchill)) in Southern Indian Lake, Manitoba. Fish. Mar. Serv. Res. Tech. Rep. No. 640. 28 p.

Ball, R.C., and D.W. Hayne. 1952. Effects of the removal of the fish population on the fish-food organisms of a lake. Ecology 33:41-48.

Barica, J. 1978. Collapses of Aphanizomenon flos-aquae blooms resulting in massive fish kills in eutrophic lakes: effect of weather. Verh. Internat. Verein. Limnol. 20:208-213.

Barko, J.W., and M.R. Smart. 1980. Mobilization of sediment phosphorus by submersed freshwater macrophytes. Freshwater Biol. 10:229-238.

Barsdate, R.J. 1967. Pathways of trace elements in arctic lake ecosystems. U.S. Atomic Energy Commission Contract AT(04-3)310PA4, Inst. of Marine Sci., Univ. of Alaska. 48 p.

_____. and V. Alexander. 1971. Geochemistry and primary productivity of the Tangle Lake system, an Alaskan alpine watershed. Arctic and Alpine Res. 3:27-41.

Bell, G., P. Handford, and C. Dietz. 1977. Dynamics of an exploited population of lake whitefish (Coregonus clupeaformis). J. Fish. Res. Board Can. 34:942-953.

Bierle, D.A. 1972. Production and energetics of chironomid larvae in ponds of the arctic coastal tundra, p. 182-186. In S. Bowen [ed.] 1972 tundra biome symposium. Hanover, New Hampshire. 211 p.

Bodaly, R.A. 1979. Morphological and ecological divergence within the lake whitefish (Coregonus clupeaformis) species complex in Yukon Territory. J. Fish. Res. Board Can. 36:1214-1222.

Brett, J.R., and C. Groot. 1963. Some aspects of olfactory and visual responses in Pacific salmon. J. Fish. Res. Board Can. 20:287-303.

Brinkhurst, R.O. 1974. The benthos of lakes. St. Martin's Press.

Brooks, J.L., and S.I. Dodson. 1965. Predation, body size, and composition of plankton. Science 150:28-35.

Bruce, W.J., and R.E. Parsons. 1979. Biology of the fishes of Ossokamanuan Reservoir, Labrador, 1976. Fish. Mar. Serv. Tech. Res. Rep. No. 836. 33 p.

Burris, R.H., and R.B. Peterson. 1978. Nitrogen-fixing blue-green algae: Their H_2 metabolism and their activity in freshwater lakes, p. 28-40. In U. Granhall [ed.], Environmental role of nitrogen-fixing blue-green algae and asymbiotic bacteria. Ecol. Bull. (Stockholm) No. 26.

Carignan, R. 1982. An emperical model to estimate the relative importance of roots in phosphorus uptake by aquatic macrophytes. Can. J. Fish. Aquat. Sci. 39:243-247.

_____. and J. Kalff. 1979. Quantification of the sediment phosphorus available to aquatic macrophytes. J. Fish Res. Board Can. 36:1002-1005.

Cattaneo, A., and J. Kalff. 1980. The relative contribution of aquatic macrophytes and their epiphytes to the production of macrophyte beds. Limnol. Oceanogr. 25:280-289.

Chellevold, J.R. 1970. The genetic relationships of intergeneric and intergeographical coregonids as determined by protein properties, p. 115-127. In C.C. Lindsey and C.S. Woods [eds.], Biology of coregonid fishes. Univ. of Manitoba Press.

Chihuly, M., D. Ward, P. Craig, and R. McMillan. 1979. Winter fisheries survey and provisional list of waterbodies along the Alaskan Gas Pipeline route (Prudhoe Bay to Yukon Territory) proposed by Northwest Alaskan Pipeline Co., L.G.L. Ecol. Res. Assoc., Inc., unpubl. report to Northwest Alaskan Pipeline Co., Fairbanks, Alaska.

Confer, J.L., and P.I. Blades. 1975. Omnivorous zooplankton and planktivorous fish. Limnol. and Oceanogr. 20:571-579.

Cooper, W.E., and L.B. Crowder. 1979. Patterns of predation in simple and complex environments, p. 257-267. In H. Clepper [ed.], Predator-prey systems in fisheries management. Sport Fishing Institute, Washington, D.C.

Cowen, C.A., M.W. Oswood, C.A. Buttimore and P.W. Flanagan. 1983. Processing and macroinvertebrate colonization of detritus in an Alaskan subarctic stream. Holarct. Ecol. 6:340-348.

Crow, M. 1976. Implications of optimal foraging theory for food web studies, p. 193-199. In S.J. Lipovsky and C.A. Simenstad [eds.], Fish food habits studies proceedings of the second Pacific Northwest technical workshop. Washington Sea Grant pub. WSG-WO-79-1, Seattle, Washington.

Cummings, K.W. 1974. Structure and function of stream ecosystems. BioScience 24:631-641.

_____. and M.J. Klug. 1979. Feeding ecology of stream invertebrates. Annu. Rev. Ecol. Syst. 10:147-172.

Darlington, J.P.E.C. 1977. Temporal and spatial variation in the benthic invertebrate fauna of Lake George, Uganda. J. Zool. (Lond.) 181:95-111.

Danks, H.V. 1978. Modes of seasonal adaptation in the insects. I. Winter survival. Can. Entomol. 110:1167-1205.

Davis, J.C. 1973. Statistics and data analysis in geology. John Wiley and Sons, Inc.

Devol, A.H., and R.C. Wissmar. 1978. Analysis of five North American lake ecosystems: V. Primary production and community structure. Verh. Internat. Verein. Limnol. 20:581-586.

Dixon, W.J., and M.B. Brown [Eds.]. 1979. Biomedical computer programs, P-series. Univ. of Calif. Press.

Drenner, R.W., and S.R. McComas. 1980. The roles of zooplankter escape ability and fish size selectivity in the selective feeding and impact of planktivorous fish, p. 587-594. In W.C. Kerfoot [ed.], Evolution and ecology of zooplankton communities. Univ. Press of New England.

Edsall, T.A. 1960. Age and growth of the whitefish, Coregonus clupeaformis of Munsing Bay, Lake Superior. Trans. Am. Fish. Soc. 89:323-332.

Eggers, D.M. 1977. The nature of prey selection by planktivorous fish. Ecology 58:46-59.

Franzin, W.G., and J.W. Clayton. 1977. A biochemical genetic study of zoogeography of lake whitefish (Coregonus clupeaformis) in western Canada. J. Fish. Res. Board Can. 34:617-625.

Godshalk, G.L., and R.G. Wetzel. 1978. Decomposition in the littoral zone of lakes, p. 131-144. In R.E. Good, D.F. Whigham, and R.L. Simpson [eds.], Freshwater wetlands, ecological processes and management potential. Academic Press Inc. Ltd.

Harris, R.J. 1975. A primer of multivariate statistics. Academic Press.

Hartman, C.W., and P.R. Johnson. 1978. Environmental atlas of Alaska. Second edition. Inst. of Arctic Envir. Engineering and Inst. of Water Resources. Univ. of Alaska.

Healey, M.C. 1978. Fecundity changes in exploited populations of lake whitefish (Coregonus clupeaformis) and lake trout (Salvelinus namaycush). J. Fish. Res. Board Can. 35:945-950.

_____. 1980. Growth and recruitment in experimentally exploited lake whitefish (Coregonus clupeaformis) populations. Can. J. Fish. Aquat. Sci. 37:255-267.

Hoagman, W.J. 1973. The hatching, distribution, abundance, growth, and food of the larval lake whitefish (Coregonus clupeaformis Mitchill) of Central Green Bay, Lake Michigan. Rep. Inst. Freshwater Res. Drottningholm 53:1-20.

Hobbie, J.E. 1973. Arctic limnology: a review, p. 127-168. In M.E. Britton [ed.], Alaskan arctic tundra. Arctic Institute of North American Tech. Paper 25.

_____. [Ed.]. 1980. Limnology of tundra ponds. Dowden, Hutchinson and Ross.

Hutchinson, G.E. 1967. A treatise on limnology. v. II. Wiley and Sons.

_____. 1975. A treatise on limnology. Vol. 1, part 1. Wiley and Sons.

Hynes, H.B.N. 1950. The food of freshwater sticklebacks (Gasterosteus aculeatus) and (Pygosteus pungitius), with a review of methods used in studies of the food of fishes. J. Anim. Ecol. 19:36-58.

Imhof, M., R. Leary, and H.E. Booke. 1980. Population or stock structure of lake whitefish, Coregonus clupeaformis, in northern Lake Michigan as assessed by isozyme electrophoresis. Can. J. Fish. Aquat. Sci. 37:783-793.

Johnson, M.G., and R.O. Brinkhurst. 1971. Assocations and species diversity in benthic macroinvertebrates of Bay of Quinte and Lake Ontario. J. Fish. Res. Board Can. 28:1683-1697.

Jonasson, P.M. 1975. Population ecology and production of benthic detritivores. Verh. Internat. Verein. Limnol. 19:1066-1072.

_____. 1978. Zoobenthos of lakes. Verh. Internat. Verein. Limnol. 20:13-37.

Kajak, Z. 1977. Factors influencing benthos biomass in shallow lake environments. Ekol. Pol. 25:421-429.

Kalff, J. 1970. Arctic lake ecosystems, p. 651-663. In M.W. Holdgate [ed.], Antarctic ecology. Academic Press.

_____. and R. Knoechel. 1978. Phytoplankton and their dynamics in oligotrophic and eutrophic lakes. Annu. Rev. Ecol. Syst. 9:475-495.

Keast, A. 1979. Patterns of predation in generalist feeders, p. 243-255. In H. Clepper [ed.], Predator-prey systems in fisheries management. Sport Fishing Institute, Washington, D.C.

Kerfoot, W.C. [Ed.]. 1980. Evolution and ecology of zooplankton communities. Univ. Press of New England.

Kessel, B., S.M. Murphy, and L.J. Vining. 1980. Waterbirds and wetlands: Chisana - Upper Tanana Rivers, Alaska, 1979. Unpubl. report to Northwest Alaskan Pipeline Co., Fairbanks, Alaska. 126 p.

Kliewer, E.V. 1970. Gillraker variation and diet in lake whitefish Coregonus clupeaformis in northern Manitoba, p. 147-165. In C.C. Lindsey and C.S. Woods [eds.], Biology of coregonid fishes. Univ. of Manitoba Press.

LaPerriere, J.D. 1981. Vernal overturn and stratification of a deep lake in the high Subarctic under ice. Verh. Internat. Verein. Limnol. 21:288-292.

Lawler, G.H. 1965. Fluctuations in the success of year-classes of whitefish populations with special references to Lake Erie. J. Fish. Res. Board Can. 22:1197-1227.

Likens, G.E., and P.L. Johnson. 1968. A limnological reconnaissance in interior Alaska. U.S. Army Cold Regions Res. Eng. Lab. Res. Rep. 239.41 p.

_____. and O.L. Loucks. 1978. Analysis of five North American lake ecosystems: III. Sources, loading and fate of nitrogen and phosphorus. Verh. Internat. Verein. Limnol. 20:568-573.

Lind, O.T. 1974. Common methods in limnology. C.V. Mosby Co.

Lindroth, A. 1957. A study of whitefish (Coregonus) of the Sundsvall Bay District. Rep. Inst. Freshwater Res. Drottningholm 38:70-108.

Lindsey, C.C. 1963. Sympatric occurrence of two species of humpback whitefish in Squanga Lake, Yukon Territory. J. Fish. Res. Board Can. 20:749-767.

_____. 1981. Stocks are chameleons: plasticity in gill rakers of coregonid fishes. Can. J. Fish. Aquat. Sci. 38:1497-1506.

Lindstrom, T. 1962. Life history of whitefish young (Coregonus) in two lake reservoirs. Rep. Inst. Freshwater Res. Drottningholm 44:113-144.

Livingstone, D.A. 1963. Alaska, Yukon, Northwest Territories, and Greenland, p. 559-574. In D. Frey [ed.], Limnology in North America. Univ. of Wisconsin Press.

Macan, T.T. 1977a. A twenty-year study of the fauna in the vegetation of a moorland fishpond. Arch. Hydrobiol. 81:1-24.

_____. 1977b. The influence of predation on the compostion of fresh-water animal communities. Biol. Rev. 52:45-70.

McPhail, J.D., and C.C. Linsey. 1970. Freshwater fishes of northwestern Canada and Alaska. Fish. Res. Board Can. Bull. No. 173. 381 p.

Merritt, R.W., and K.W. Cummins [Eds.]. 1978. An introduction to the aquatic insects of North America. Kendall/Hunt Publishing Co.

Mills, K.H., and R.J. Beamish. 1980. Comparison of fin-ray and scale age determinations for lake whitefish (Coregonus clupeaformis) and their implications for estiamtes of growth and annual survival. Can. J. Fish. Aquat. Sci. 37:534-544.

Moreau, G., et C. Barbeau. 1979. Differenciation de populations anadromes et dulcicoles de Grands Coregones (Coregonus clupeavormis) par la composition minerale de leurs ecailles. J. Fish. Res. Board Can. 36:1439-1444.

Murdoch, W.W., S. Avery, and M.E.B. Smyth. 1975. Switching in predatory fish. Ecology 56:1094-1105.

Murphy, S.M., B. Kessel and L.J. Vining (in press). Waterfowl populations and limnologic characteristics of taiga ponds. J. Wildl. Manage.

Nilsson, N.A. 1958. On the food competition between two species of Coregonus in a north-swedish lake. Rep. Inst. Freshwater Res. Drottningholm 39:146-161.

O'Brien, W.J., N.A. Slade and G.L. Vinyard. 1976. Apparent size as the determinant of prey selection by bluegill sunfish (Lepomis macrochirus). Ecology 57:1304-1310.

Odum, W.E., and R.T. Prentki. 1978. Analysis of five North American lake ecosystems: IV. Allochthonous carbon inputs. Verh. Internat. Verein. Limnol. 20:574-580.

Oliver, D.R. 1968. Adaptations of arctic Chironomidae. Ann. Zool. Fenn. 5:111-118.

_____. D. McClymont, and M.E. Roussel. 1978. A key to some larvae of Chironomidae (Diptera) from the Mackenzie and Porcupine River watersheds. Fish. Mar. Serv. Tech. Rep. No. 791. 73 p.

Otto, C., and B.S. Svensson. 1981. How do macrophytes growing in or close to water reduce their consumption by aquatic herbivores? Hydrobiol. 78:107-112.

Pennak, R.W. 1978. Freshwater invertebrates of the United States. Second edition, John Wiley and Sons.

Porter, K.G. 1977. The plant-animal interface in freshwater ecosystems. Am. Sci. 65:159-170.

Ringler, N.H. 1979. Prey selection by benthic foragers, p. 219-229. In H. Clepper [ed.], Predator prey systems in fisheries management. Sport Fishing Inst., Washington, D.C.

Ryder, R.A., S.R. Kerr, K.H. Loftus, and H.A. Regier. 1974. The morphoedaphic index, a fish yield estimator: review and evaluation. J. Fish. Res. Board Can. 31:663-688.

Sampson, R.J. 1978. Surface II graphics system: series on spatial analysis; No. 1, Kansas geological survey, Lawrence, Kansas.

Schoener, T.W. 1971. Theory of feeding strategies. Annu. Rev. Ecol. Syst. 2:369-404.

Seghers, B.H. 1975. Role of gill rakers in size-selective predation by lake whitefish, Coregonus clupeaformis (Mitchill). Verh. Internat. Verein. Limnol. 19:2401-2405.

Selkregg, L.L. 1976. Alaska regional proviles: V. VI: Yukon region. Arctic Environmental Info. Data Center, Univ. Alaska, Anchorage, Alaska. 346 p.

Sondergaard, M. 1981. Loss of inorganic and organic carbon by ^{14}C-labelled aquatic plants. Aquat. Bot. 10:33-43.

Soszka, G.J. 1975. Ecological relations between invertebrates and submerged macrophytes in the lake littoral. Ekol. Pol. 23:393-415.

Spindler, M.A., and B. Kessel. 1977. Wetland bird populations in the upper Tanana River Valley, Alaska, 1977. Univ. Alaska Museum unpubl. report to Northwest Alaskan Pipeline Co., Fairbanks, Alaska. 71 p.

Stenson, J.A.E. 1979. Predator-prey relations between fish and invertebrate prey in some forest lakes. Rep. Inst. Freshwater Res. Drottningholm 58:166-183.

Strickler, J.R. 1975. Intra- and interspecific information flow among planktonic copepods: receptors. Verh. Internat. Verein. Limnol. 19:2951-2958.

Svardson, G. 1952. The coregonid problem. IV. The significance of scales and gillrakers. Rep. Inst. Freshwater Res. Drottningholm 33:204-232.

_____. 1965. The coregonid problem. VII. The isolating mechanisms in sympatric species. Rep. Inst. Freshwater Res. Drottningholm 46:95-123.

Tack, S.L. 1980. Distribution, abundance and natural history of the Arctic grayling in the Tanana River drainage. Alaska Dept. of Fish and Game, Fed. Aid in Fish Restoration, Completion Rep., 1971-1980, Project F-9-12, (R-I): 32 p.

Tsuyuki, H., J.F. Uthe, E. Roberts, and L.W. Clarke. 1966. Comparative electropherograms of Coregonus clupeaformis, Salvelinus namaycush, S. alpinus, S. malma, and S. fontinalis from the family Salmonidae. J. Fish. Res. Board Can. 23:1599-1606.

Urban, E. 1975. The mining fauna in four macrophyte species in Mikolajskie Lake. Ekol. Pol. 23:417-435.

Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37:130-137.

Vollenweider, R.A. 1968. Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication. Paris, Rep. Organization for Economic Cooperation and Development. DAS/CSI/68.27. 192 p.

Walker, E.M. 1953. The Odonata of Canada and Alaska. V. I. Univ. of Toronto Press.

Wallace, R.E. 1948. Cave-in lakes in the Nabesna, Chisana, and Tanana river valleys, eastern Alaska. J. Geol. 56:171-181.

Welch, E.B. 1980. Ecological effects of waste water. Cambridge Univ. Press.

Werner, E.E., and D.J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (Lepomus macrochirus). Ecology 55:1042-1052.

Wetzel, R.G. 1975. Limnology. Saunders.

Whitledge, T.E., S.C. Malloy, C.J. Patton, and C.D. Wirick. 1981. Automated nutrient analysis in seawater. U.S. Dept. of Energy Contract No. DE-AC02-76CH00016. 158 p.

Wiggins, G.B. 1977. Larvae of the North American caddisfly genera (Trichoptera). Univ. Toronto Press.

Zar, J.H. 1974. Biostatistical Analysis. Prentice-Hall, Inc.

Zaret, T.M. 1980. Predation and freshwater communities. Yale Univ. Press.